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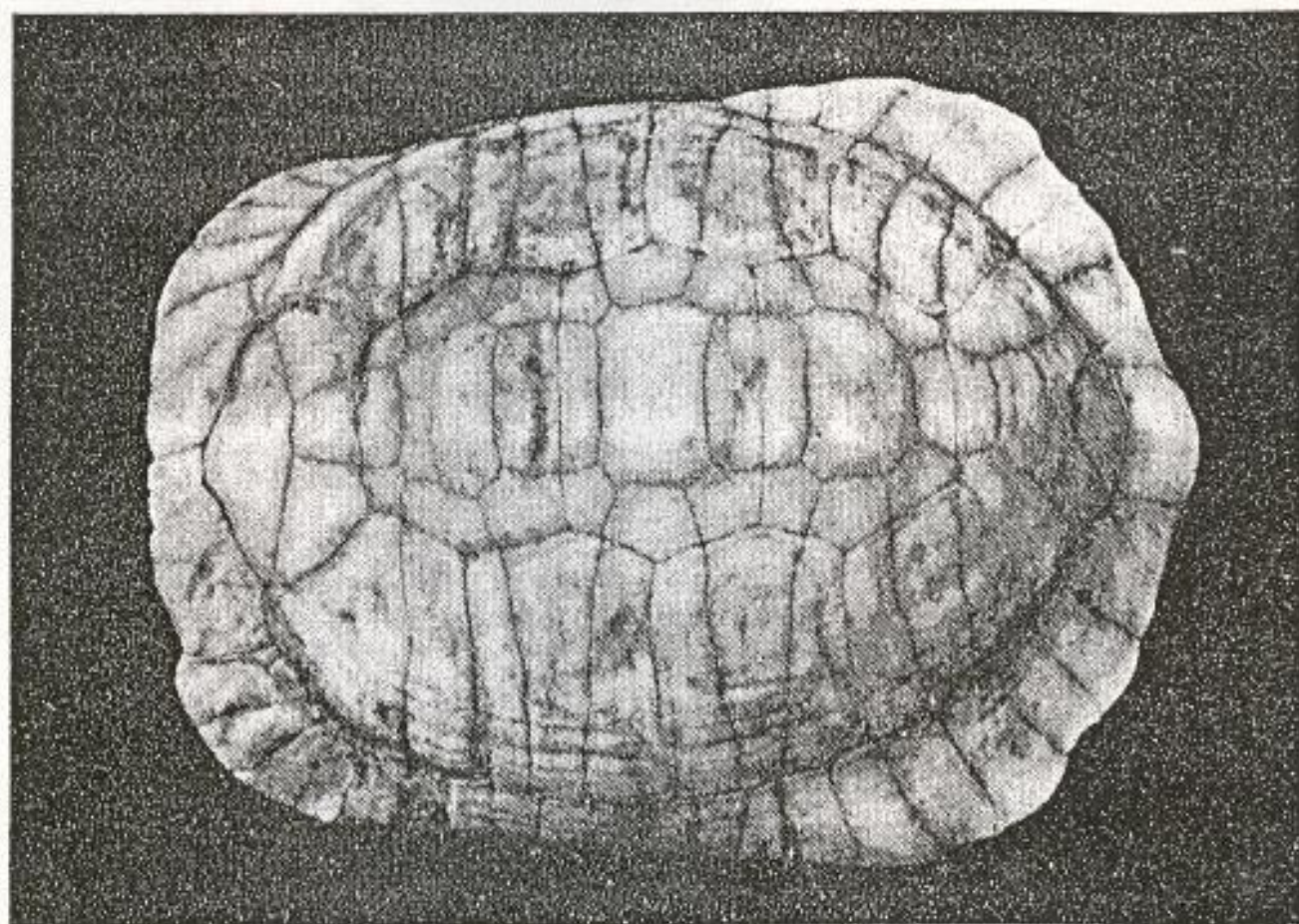
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TAXONOMY: BIOLOGY: ECOLOGY:
CONSERVATION

of the Tortoises and Turtles of the World

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Tortoises of north Africa; taxonomy, nomenclature, phylogeny and evolution with notes on field studies in Tunisia

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Abstract

This report describes the history and effects of the tortoise trade, field techniques used in surveying north African tortoises and describes the non-*Testudo* suprapygial structures encountered in the region. The significance of this finding for taxonomy and conservation is discussed. Some of the standard criteria for differentiating African genera are also analysed and questioned. A new genus *Furculachelys* is proposed.

KEYWORDS:- *Testudo* - *Geochelone* - *Homopus* - Osteology - Taxonomy - Evolution - *Testudo graeca* - Distribution - Palaeontology - Africa - *Testudo hermanni* - *Testudo horsfieldi* - *Furculachelys nabeulensis* (genus & species nov.).

A brief history of the n. African Tortoise Trade

Of all localities inhabited by land tortoises, none (with the possible exception of the Galapagos) have been so consistently heavily plundered by human predators as north Africa; precise numbers of animals collected from this region to supply the European pet trade are unfortunately not available, but from individual records which have been published it is clear that many tens of millions of animals have been taken from the wild during a period of intense trading dating back to the turn of the century.

The early trade was not extensive, and tortoises were prized as rare and valuable curiosities. Most of these animals were brought back to Europe individually, or at most in very small numbers, by sailors. One of the most famous animals acquired in this way was the tortoise of the great naturalist Gilbert White of Selborne. This tortoise was purchased "from a sailor" in Chichester for 2/6^d in 1740 - a very considerable sum of money in those days. The present author has shown that this tortoise was almost certainly captured in the vicinity of Algiers (Highfield & Martin, 1989). Another tortoise which must have entered by a similar route was that of Archbishop Laud, who maintained a tortoise in London from 1628 onwards. This tortoise apparently survived until the mid 1700's when it was unfortunately accidentally killed by a careless gardener.

The earliest documented accounts of commercial importation begin to appear around 1886 when in Norfolk, England, Sir Peter Eade (cited in Loveridge & Williams, 1957) records purchasing some tortoises from a street trader in Norwich (subsequently detailing

their habits in a local zoological journal), and by 1894 the French naturalist Olivier was reporting the first bulk shipments departing Algiers destined for Marseille.

By the turn of the century, the trade was numbered in thousands annually; by the mid-20th century numbers had risen to hundreds of thousands annually. The only respite for the tortoises occurred during the second World War when exports ceased temporarily.

Lambert¹⁴ (1969) quotes figures of more than 300,000 tortoises being exported from Morocco alone to Britain each year for pets in the period after the War; similarly enormous quantities of tortoises were extracted from Algeria, with additional large numbers being taken from Tunisia and Libya. Not only Britain received these shipments; there was a persistent demand for north African tortoises throughout Europe. France, Germany, Holland and other European countries annually consumed hundreds of thousands of wild tortoises thus depleting natural populations on a scale almost beyond imagination.

During this period there was no attempt to conserve these animals; they were viewed as expendable and irrelevant commodities usually sold for a few pennies each from street stalls or markets throughout Europe.

Lambert (1976) noted that since the U.K Animals (*Restriction of Import*) Act 1964 required records of numbers imported to be kept for the first time 2,023,580.00 Mediterranean spur-thighed tortoises were imported into the U.K with 68.5% originating in Morocco.

Lambert (1969) describes the process of collection and shipment;

"Until a few years ago common tortoises *Testudo g. graeca* - in Arabic *facron* - were collected in Morocco mainly from the region of Casablanca, the exporting centre. Today they are very scarce in this region, and to satisfy a trade which every year exports over 300,000 tortoises to Britain they are collected all over Morocco. The collectors are mostly shepherds who bring the tortoises in to provincial collecting centres along with their animals on the weekly market days and get about six-pence for each one. The tortoises are then sent in sacks, in vans or on top of public buses, to Casablanca, from where, because they are too heavy for airfreight - 3,000 tortoises weigh about a ton - they are sent by sea, packed in baskets stowed upright on deck. The seamen, with uncertain humanity, spray the baskets with sea water to prevent the creatures from roasting in the sun. In this way, between 10,000 and 25,000 tortoises are dispatched to London once a fortnight".

Before packing, the same author also noted that tortoises were routinely poorly handled and were;

"frequently picked up by their limbs, often leading to joint dislocation. If tortoises perished while being held by the dealers, there was no financial loss for the carapaces of the corpses could be converted to banjos for sale as tourist curios" (1).

The fate which awaited these creatures upon arrival was often appalling; very few survived their first hibernation in captivity. Blatt & Muller (1974) in a survey conducted in Germany suggested that over 82% died within a year, and in the U.K Lawrence (1987 & 1989) conducted a 4 year survey of 606 tortoises purchased as pets of which by the end of

(1) This trade still unfortunately persists; recent reports cite such objects being offered for sale on Tenerife, Mallorca, Gibraltar, the Canary Islands and in Morocco.

the study 404 had died in hibernation and another 137 had perished from other causes. Of this last group, post mortem results indicated 57 had died from effects associated with inanition. Some additional causes of mortality affecting tortoises purchased by the public as pets have earlier been described by the present author (Highfield, 1987).

A point not made by Lawrence (1989) but which is relevant is that the species covered by his survey were not *T. graeca* L. 1758 from n. Africa, but *T. ibera* PALLAS 1814 from Turkey and *T. hermanni* GMELIN 1789 from Yugoslavia - both species which are (in this authors experience) considerably easier to maintain in captivity than the much more delicate and environmentally sensitive n. African species; compare natural bioclimatic range of *T. ibera*, *T. hermanni* with n. African *T. graeca* (Lambert, 1988) to climates of importing countries where greatest disparity in terms of temperature and biotype is seen in respect of the n. African origin tortoises. This factor may account for the more rapid deaths of the animals featured in the Blatt and Muller (1974) survey which took place before trade restrictions were imposed upon tortoises from Morocco and which as a consequence was based largely upon animals of n. African origin whereas Lawrences (1987 & 1989) surveys were based upon tortoises of more northerly origins.

Those that remained unsold at the end of the import season were treated with scant regard by traders who considered them as liabilities to be disposed of by whatever means possible. Noel-Hume (1954) records an instance during 1952 when a gang of boys discovered a basket full of dying tortoises (discarded by a dealer) on a bomb site; some they set up as targets at which to throw bricks, the rest they hurled to their deaths against walls. In another incident, 250 'surplus' n. African tortoises were abandoned in a London street by an unscrupulous dealer - an event which provoked questions to be asked in Parliament and unfortunately unsuccessful demands to be made for the trade to be controlled (Vodden, 1983).

The entire history of the tortoise trade is truly a sickening indictment of mankind's mistreatment of animals and disregard for the natural world.

Even as late as 1980 live tortoises could be purchased for food at many fishmongers shops in France (*Bulletin de la Societe Herpetologique de France*, No.14) and this particular aspect of the trade was eventually only suppressed on health (not welfare or conservation) grounds, it being pointed out that in a survey of 56 *T. graeca* from the Tangiers region of Morocco that 96% of those from field habitats and 64% of those from urban habitats carried *Salmonella* organisms. Applications to import 700,000 *T. graeca* & *T. hermanni* into France were recorded in 1979 alone.

Such persistent and massive extractions of potential breeding stock from the wild has obviously had extremely detrimental effects upon natural populations; precise data is again hard to come by as the trade was never properly monitored and in most areas no surveys either before or after have ever been carried out. Anecdotal evidence however suggests that in many areas where once tortoises were "very common" they are now rarely sighted.

Lambert (1981) reported a sighting frequency of *T. g. graeca* in trade collected areas of N. W. Africa of 0.3 man-h⁻¹ compared to 3.3 man-h⁻¹ for *Testudo (graeca) ibera* in largely uncollected populations in western Turkey. This correlates to a relative density of uncollected areas in western Turkey of 11.6 times that of trade collected n. African localities.

An estimated annual population decline rate of 3.1% over the 80 plus years of trade

collection has therefore resulted in a massive depletion of wild tortoises. Lambert (1979) suggests the net effect of collecting *Testudo graeca* in Morocco may have reduced pre-trade population levels by as much as 86%.

This figure, appalling though it is, hides an even greater tragedy; for collection activities were not evenly distributed, but generally were more intensive in certain areas than in others e.g for Moroccan data see Lambert (1969). In certain of these areas, individual tortoise populations have almost certainly been rendered completely extinct and in others pushed to the very brink of extinction.

Iverson (1982) has in addition pointed out that tortoises have a low annual biomass production resulting in a high degree of sensitivity to population disturbance and consequent poor recovery abilities from such activities as trade collection. Where disturbance is severe any recovery will be very slow, or may not be possible at all.

In 1978 Morocco ratified C.I.T.E.S (Convention on International Trade in Endangered Species - Washington Convention 1973) and the export of tortoises from there finally ceased after decades of intense exploitation. The pet trade in Europe still demanded tortoises however, and turned increasingly to Turkey and Yugoslavia to meet its requirements. From these countries, *Testudo ibera* PALLAS 1814 and *Testudo hermanni boettgeri* MOJSISO-VICS 1889 were collected in large numbers in place of the no longer available north African species. Eventually, this trade too ended in 1984 following the Council of European Community regulation EEC no. 3626/82 prohibiting entirely import or any other form of trade in Mediterranean tortoises from 1st January 1984.

The author recalls witnessing tray loads of sad tortoises on sale in dingy pet shops in the years before the trade finally ceased. It is a sight one hopes never to see again.

Despite the welcome end of trade collecting and mass export of Mediterranean tortoises, these animals remain under intense pressure in many areas from the expansion of human encroachment activities such as tourism and intensification of agricultural practices (Honegger, 1981 and Lambert, 1984). The question of toxic pesticides (principally Dieldrin, Malathion and Fenitrothion) as a potential further contributory factor in decline has also been raised; however Lambert (personal communication) indicates that to date this does not appear to represent a major threat. It is a threat which may increase however and the situation in this respect does require careful monitoring.

Field techniques;materials & methods

The technique of gathering data from wild tortoises is comparatively simple and has to some extent attained a level of standardisation among researchers. There are differences of approach which must be considered in respect of field-work as opposed to museum studies however. Time is often of the essence in field situations and physical difficulties often preclude the use of certain laboratory instruments. The following parameters were recorded and methods adopted during the present study.

Weight

Weight was measured using a range of spring balances graduated in grammes and kilogrammes. Weights up to 200g were measured using a 'Salter' precision spring balance graduated in 2g increments, weights over 200g were taken using a balance graduated in 10g increments. A light plastic bag was used to hold the animals. All balances were

calibrated against known weights. It is necessary to be aware that acute weight-loss can occur due to stress induced urination initiated by handling.

Length

Straight carapace length (SCL or *L*) was measured using a simple "tortometer" constructed by fixing a millimeter plastic ruler on a wooden mount with its anterior end terminated with a fixed perpendicular wooden block at the zero mark. The tortoise is placed on the ruler with the nuchal-gular region butted firmly against the zero block and a second (movable) block placed against the supracaudal scute and the length noted.

Length over the curve (LoC) is recorded using a flexible tape measure from nuchal to supracaudal.

Width and other dimensions

All other dimensions are recorded using a precision dial caliper graduated from 0-150mm. This should be rust-proof for durability. The same instrument is useful for measuring eggs.

Environmental recording

The altitude at which specimens are located, plus details of both open and shade temperature together with ambient humidity should always be recorded. This data can prove extremely useful when analysed later and compared with activity or behavioural observations.

We normally noted three temperature parameters for each tortoise sighting; air temperature (in shade, at 150mm above ground level), ground temperature (by inserting the probe 10mm into the substrate) and a tortoise body temperature (*per cloaca*).

Population density - sighting frequency

It is often very difficult to estimate with any real accuracy the number of tortoises in any given area. There are a number of reasons for this which include the ability of the animals to hide themselves, the type of terrain often preferred, and the limited number of hours each day when activity occurs.

It is much easier to locate animals during activity periods than it is when they are at rest. In more arid habitats tortoises can often be located by sound as they move over dry leaf litter. However, where the ground is moist and the plant cover green very little sound is produced by the tortoises movement. In north Africa an added danger to searchers is the likely proximity of highly lethal poisonous snakes - this is certainly an inhibiting factor insofar as hand searches of vegetation are concerned.

Some methods of assessing tortoise population densities have been discussed in detail by other authors (*e.g see* Bury & Luckenbach, 1977, Lambert 1981 & 1982, Hailey, Pulford & Stubbs 1984, and Stubbs, Hailey, Pulford & Tyler 1984). Our own methods are presently based upon man-hours per tortoise sighted. This is not a precise method by any means (it is heavily influenced by the skill and experience of the observer among other factors), but it does provide a general indication of numbers present in a particular area.

Dimensional data recording

Various authors have proposed different methods and criteria for obtaining and recording data from turtle shells (Auffenberg 1976; Grubb 1971; Schleich 1984). It is normally our

practice when time permits to record longitudinal and transverse measurements from each carapace scute individually. Longitudinal measurements of the plastron sutures are also recorded and expressed as a 'plastral formula' (Loveridge & Williams 1957). However, this is a very time consuming process (it can take an hour or more to extract a full set of data from each animal) and therefore is not always practicable under field conditions.

The following dimensions are especially useful for comparison and diagnostic purposes and should always be recorded.

- Straight-line carapace length (SCL or *L*)
- Carapace length over curve (*LoC*)
- Median body width (*Mw*)
- Maximum width at marginals (*MwM*)
- Body width as *M*¹-*M*² (front) marginal suture (*Fw*)
- Maximum carapace height at *V*²-*V*³ (*Ch*)
- Weight (*W*)
- Plastral suture lengths *P*¹, *P*², *P*³, *P*⁴, *P*⁵ and *P*⁶
- Post anal gap (*PaG*)

NB:- In our own field record system the abbreviations *P*¹ = Intergular, *P*² = Humeral, *P*³ = Pectoral, *P*⁴ = Abdominal, *P*⁵ = Femoral and *P*⁶ = Anal suture, '*V*' = Vertebrae, '*C*' = Costals and '*M*' = Marginals (peripherals).

A very useful ratio is obtained by dividing the straight-line carapace length (*L*) by the maximum carapace height (*Ch*). The resulting index in our experience can be of considerable diagnostic value (Highfield & Martin, 1989). The width of the posterior carapace marginals (*MwM*) compared to the median and frontal carapace width (*Fw*) is another very useful feature diagnostically and can also indicate the sex of a specimen (Highfield & Martin, 1989).

Field records & observations - Tunisia

Biotypes of n. African tortoises in present day Tunisia

The highest concentrations of tortoises occur in the north and along the Sahel coastal region. The annual rainfall is highest in the north >1000mm and lowest in the south <125mm average. The precipitation in the southern interior is even lower, vast areas comprising no more than arid sandy desert. No tortoises occur in such habitats.

Northern Tunisia

Generally speaking, this region comprises a series of ridges and valleys which support a dense growth of cork and holm oak forest. Much of the area is above 600m and the highest peak is Djebel Chambi at 1519m. At lower levels, particularly in coastal sites where the vegetation has been most affected by man, extensive areas of maquis and *Opuntia* scrubland occur supporting broom, buckthorns, lavender, thyme and similar aromatic shrubs. This biotype is in many ways typically modern Mediterranean. In the areas of high

precipitation evergreen woodland predominates and it is these locations which tend to be most favoured by tortoises. These are also the areas least affected by the activities of mankind. The region of Ain Draham and Tebour Souk has the highest recorded annual rainfall of any location in n. Africa (>1050mm p.a) and is ideal habitat for land tortoises in addition to providing an equally good habitat for aquatic chelonians.

Coastal Tunisia - the Sahel

The coastal plains of the Cap Bon and from Hammamet to Sousse are also typically Mediterranean in vegetation although degeneration from original primal forest is very advanced locally with extensive maquis, garigue and steppe conditions. Annual precipitation varies from circa 420mm in Tunis gradually decreasing to circa 300mm in the south. The sandy soil retains moisture well however, and a good covering of plant growth is supported. The rainfall is also supplemented with regular dew deposits and sub-soil water is also available in most locations. This area supports a productive agriculture. Tortoises are found in undisturbed habitats and on the periphery of traditionally cultivated olive and citrus groves.

The south of Tunisia

In the extreme south rainfall is very unpredictable and ranges from 150mm - 200mm along the narrow coastal band but elsewhere falling to less than 125mm. The vegetation in most areas is sparse but the land does support a very considerable number of date palms which are a major agricultural commodity. Tortoises are rare in this region compared to the north, but do occur in limited numbers as noted by Anderson (1892) and confirmed by Lambert (1983 and personal communications).

Valuable historical information on tortoise distribution in Tunisia is provided by Mayet (1903), by Mosauer (1934) who lists observations in the Rades, Sidi bou Ali and Kairouan regions, by Gadeau de Kerville (1908) and by M. Blanc (1935) who notes the presence of tortoises in the Khroumirie, Cap Bon, Kelibia, Sousse, Kairouan and region of Tunis. Other interesting accounts are provided by Boulenger (1891) who cites *T. graeca* in the ruins of Zarzis, by König (1892), Olivier (1896), Anderson (1892) and by Seurat (1922 and 1927). Additional recent data is provided by Blanc (1978) and Highfield (1990^a).

In December 1989 and April 1990 we recorded data from some 35 tortoises in Tunisia; of these, approximately half were captive specimens (usually kept as pets by villagers). The rest were recorded in the field. In the latter case, over 120 man-hours were expended searching previously recorded sites. The average find rate was 1 tortoise per 9 man-hours searching. The best site located yielded only 4 tortoises for 18 man-hours searching. This suggests that even in established and obviously suitable habitats the population density is now very low indeed. Other researchers who have visited Tunisia recently have also reported that tortoises are now scarce, despite many sympatric species (e.g. *Tarentola mauritanica*, *Discoglossus pictus*, *Ophysops occidentalis*, *Psammotrogon algericus*, *Natrix maura*, *Lacerta lepida* and *Bufo* spp.) being located with relative ease (Bruekers, personal communications). Unfortunately, tortoises continue to be collected from these sites for (illegal) sale to foreign tourists; both Hammamet and Sousse are centres for this activity. Tortoises are also killed, dried in the sun and varnished to produce 'souvenirs' for sale to foreign visitors. Such items can be openly purchased in many tourist centres in the country. In 10 minutes of surveying the shelves of one tourist shop alone we saw more dead 'souvenir' specimens for sale than we managed to locate live specimens in two weeks of

intense searching. Many of the dead tortoises on display were juveniles.

Some general details of Tunisia's unique fauna of land tortoises were provided previously (Highfield, 1990^a). As additional data has now been collected and analysed, a more complete picture of these remarkable creatures is beginning to emerge.

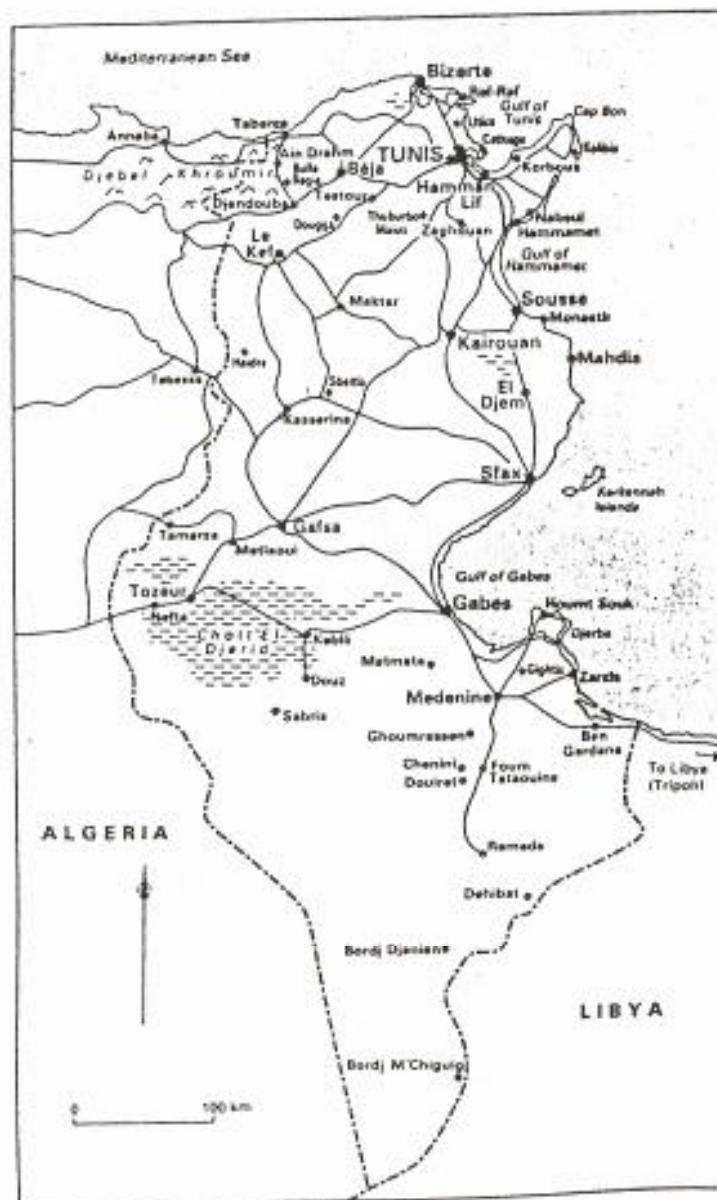
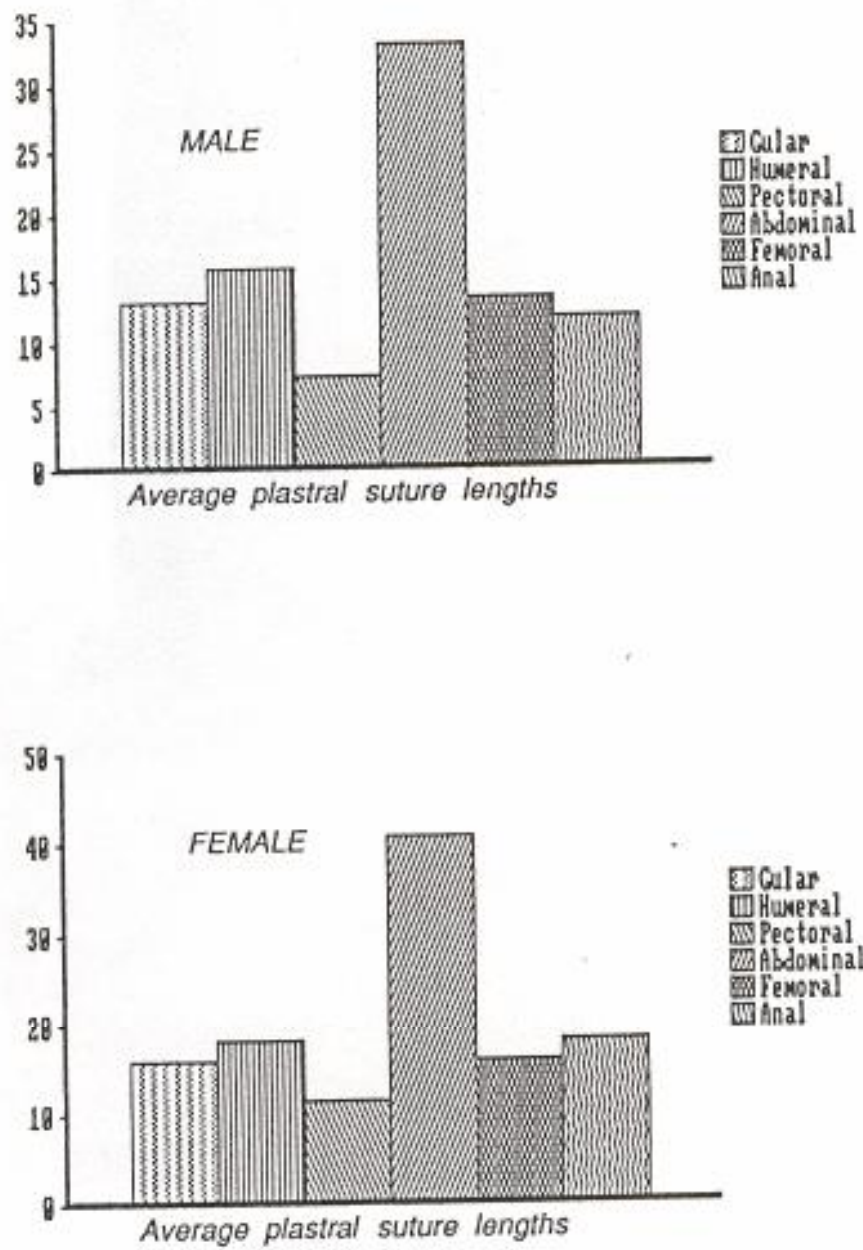


Fig.1 Tunisia

Figure 2. Dimorphism in plastral scute mid-line sutures



Sexual dimorphism- diagnostic characters

This is particularly striking in Tunisian coastal zone tortoises, where females weigh considerably more than males of equivalent age, even very mature specimens of which are extremely small. Typically, a sexually mature adult male weights approximately 372g compared to an average female at 607g. The heaviest male we encountered in the entire series weighed 550g compared to the heaviest female at 750g.

Length & height

The carapace length and height is also strongly dimorphic; adult females typically measuring 134mm SCL (straight carapace length) compared to a typical adult males 117mm SCL. Males have a low vaulted carapace, typically *circa* 54.23mm high, whilst females typically attain *circa* 71.55mm. If a measurement is taken over the curve using a flexible ruler, females average 175.45mm and males 148.18mm. If a length-height ratio is prepared by dividing the SCL by the maximum carapace height, the average index for males is 2.16 and the average for females 1.87.

Width

The transverse median width of the carapace typically *approaches or is equivalent* to the maximum transverse width of the posterior marginals in the case of females, but in the case of males the posterior marginals typically project beyond the transverse median carapace width by several millimeters.

Supracaudal

Another extremely useful indicator is the supracaudal shape, which in males is posteriorlaterally projected and introflexed on its anterior face. In female specimens the supracaudal is reduced by comparison and lacks the anterior ventral introflexion (*fig. 3*).

Plastral sutures

During the course of routine morphometric data analysis, quite by chance it was noted that the plastral formulas of male and female specimens differed consistently; this is presented graphically (*figure 2*). This is interesting, as the plastral formula (or sequence of length reduction in the mid-line sutures of the plastron) is often cited as a fixed character within a taxon.

Typically, where the femoral suture is subequal to the anal suture = Female, and where the femoral suture is equal to or exceeds the anal suture = Male. The overall relative dimensions are also very different with the average for males as P^5 (femoral) = 13.36mm and P^6 (anal) = 11.95mm ; for females the respective dimensions are P^5 = 16mm and P^6 = 18.14mm reflecting the larger overall carapace size and body mass of female specimens.

Post anal gap

It was also noted that the PaG of the female specimens was invariably less than that of the males - typically 15.59mm in females compared to 18.07 in males. There is a relatively high degree of xiphiplastral kinesis in both sexes, the xiphiplastra of females not noticeably more pliant than that of males.

Egg morphology

One of the most remarkable features of the Tunisian coastal tortoise is the incredibly tiny

dimensions of their eggs; Mayet (1903) measured some at just 15mm X 13mm, dimensions we confirmed in many discussions with local people. These dimensions should be compared with typical egg sizes from other tortoises (table 1).

Our information is that the females can lay up to 12 of these tiny eggs, but more often lay clutches of 6-8. This in itself is quite remarkable, as most other small tortoises (e.g. *T. kleinmanni*, *Homopus* etc.) lay fewer, but larger eggs. Large clutch densities are often associated with high levels of predation, and certainly one would expect such minute hatchlings to be especially vulnerable.

It should be noted that we qualify our comments to apply only to the "Tunisian coastal tortoise" - for we have reason to believe that other entirely different tortoises also exist in separate geographic populations within Tunisia. These other tortoises almost certainly are not closely related to the tiny specimens which inhabit the coastal zone and in our opinion, must comprise separate species.

The evidence in the literature for this is intriguing. Chaigon (1904) recorded finding three ellipsoid eggs "the size of a pigeons egg" inside a tortoise which he consumed for dinner. A large female recorded from Maktar in 1890 laid a total of 7 eggs which measured 28 X 36mm (Domergue, 1899). Another set of measurements made by Gadeau de Kerville (1908) list egg dimensions from 24.5 to 31 x 31.5 to 38.5mm. The laying female measured 202mm, which is far in excess of any specimen recorded in the coastal zone. Additionally, we doubt that the small coastal zone females could carry a clutch of between 4-8 eggs of such size, and certainly could not carry as many as 12 as reported by Mayet (1903). Our discussions with local people also resulted in reports of "very big" tortoises living in some distant (north-western) inland forests. We believe that these large tortoises may be related to some of the large specimens which occur in neighboring Algeria.

We certainly feel justified in concluding that geographically separate populations which consistently each lay eggs as diverse as 15 X 13mm and 28 X 36mm are unlikely to belong to the same species as such a range of deviation is unknown within a single taxon where the standard deviation within a single taxon for circum-mediterranean tortoise species is typically ± 2.00 mm in length and ± 1.25 mm in width (Highfield, 1990^a and in press).

A *Malacochersus* female in our own collection regularly produces eggs measuring (on average) 42mm x 29mm, however in this case the posterior lobe opening measures some 29mm long by 33mm wide.

The most significant feature of our Tunisian coastal specimens is the combination of minute egg size plus the clutch density. A combination which is unknown in any other terrestrial tortoise. The inland populations, which produce the very large egg, for the moment remain a mystery.

Further research aimed at establishing the phylogenetic relationships and identity of the inland populations is proposed.

Hatchlings & juveniles

Clearly, the egg dimensions of the coastal zone tortoises impose size restrictions upon the hatchlings. Our experience from captive breeding north African and circum-mediterranean species suggests that the carapace length of emerging hatchlings tends to be equal to or ± 3.00 mm greater than the maximum length of the egg for egg sizes below 30mm in length and approximately equal to or sub-equal to the longitudinal length of the egg for eggs

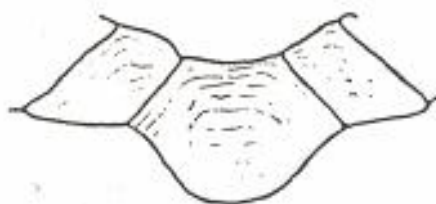
which measure in the range 30-40mm. The excess few millimeters above the egg length in smaller eggs are accounted for by the plastral fold present on hatchlings. We have noted that in some species hatchling orientation within the egg is typically longitudinal, and in others it is typically transverse.

This would suggest that the probable hatchling size of the Tunisian coastal tortoise is in the range circa SCL 15-17mm. This should be compared to a hatchling size of circa 33mm SCL for Algerian *F. whitei*, circa 27mm SCL for Moroccan *T. graeca*, 32mm SCL for *T. hermanni boettgeri* and an estimated possible hatchling SCL of circa 33-35mm SCL for the (currently unknown) inland populations of Tunisia.

The smallest tortoise we found was circa 45mm SCL and weighed circa 28g. We found this tortoise in the verge of a ploughed field adjacent to a well vegetated hillside where several adult tortoises have been recorded. There were four clear growth rings, and we would estimate the age of the tortoise at 18 months to 2 years. Locating juveniles at or below this size presents obvious difficulties for searchers.

Other, somewhat older juveniles were located, photographed and recorded. These included an immature male of 78mm SCL and two young females at 96mm SCL and 67mm SCL.

Fig. 3 Supracaudal shape; Male (left) Female (right)



MALE



FEMALE

African land tortoises; some diagnostic criteria at Genus level

Carapace morphology and structure

Suprapygal morphology

The structure of the pygal and suprapygal bones of the carapace of chelonians is an important diagnostic character which may be employed to distinguish between genera and to provide an indication of evolutionary descent and phylogenetic relationships (Loveridge & Williams 1957; Crumly 1984 ; Meylan & Auffenberg 1986). The following are the generally accepted pygal characters of some currently recognised African cryptodiran genera;

GEOCHELONE Fitzinger 1835

Two suprapygals, the anterior larger, bifurcating posteriorly to embrace the smaller posterior element, which (on post-Eocene forms) is crossed near its middle by the sulcus between the fifth vertebral and the supracaudal. Concerning this genus, Loveridge & Williams (1957, p. 222) remark that "earliest of these (specialisations) are a thickened, produced gular region and the peculiar pygal pattern with the first suprapygal embracing a second smaller one, both already present in *Hadrianus* of the Eocene" ⁽²⁾. Both conditions are relevant to the new tortoises from n. Africa to be described herein. Of extinct genera, a similar suprapygal structure was shared with *Hesperotestudo* .

HOMOPUS Dumeril & Bibron 1834 ⁽³⁾

Two suprapygals, the anterior larger, bifurcating posteriorly to embrace the smaller element which is adjacent to, but not crossed by, the sulcus between the fifth vertebral and the supracaudal (Loveridge & Williams, 1957, p. 353).

TESTUDO Linnaeus 1758

Frequently a single suprapygal, if two, they are typically separated by a straight transverse suture (Loveridge & Williams, 1957, p. 255).

PSAMMOBATES Fitzinger 1835

Typically a single suprapygal, if two, then separated by a straight transverse suture (Loveridge & Williams, 1957, Pritchard, 1979).

CHERSINA Gray 1831

Suprapygal typically single, if at all divided then with a straight transverse suture (Loveridge & Williams, 1957).

MALACOCHEUS Lindholm 1929

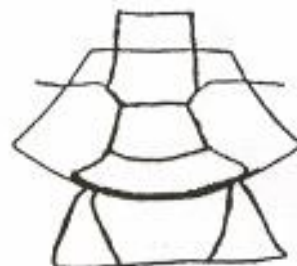
Typically a single suprapygal (Loveridge & Williams, 1957).

⁽²⁾ Note, however that *Hadrianus* was synonymised into *Manouria* by Auffenberg (1971) as "no characters differentiated one from the other".

⁽³⁾ Bour (1988) has pointed out that Mertens & Wermuth (1977) cited the incorrect date (1835) for the erection of the new genus of *Homopus* by Dumeril & Bibron. Bour also points out that the type species of *Homopus* is *T. areolata* THUNBERG 1787 a result of later designation by themselves (Dumeril & Bibron 1835) and not by Fitzinger (1843) as is usually cited.



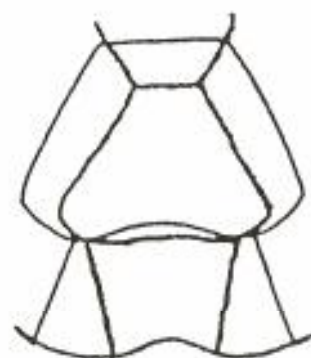
1. *Geochelone pardalis*



2. *Testudo graeca graeca*



3. *Homopus signatus*



4. *Psammobates t. tentorius*

Fig. 4 Suprapygial structures of African land tortoise genera (redrawn after Loveridge & Williams, 1957).

KINIXYS Bell 1827

Suprapygals one or two, if two typically separated by a straight transverse suture (Loveridge & Williams, 1957).

IMPREGNOCHELYS Meylan & Auffenberg 1986 (Miocene, extinct)

Two suprapygals, a rounded second suprapygal resting within a rounded notch in the pygal with the posterior sulcus of the fifth vertebral scute at its dorsal edge (Meylan & Auffenberg, 1986).

The presence or absence of the *Geochelone* or *Homopus* type pattern, that is, a twin suprapygal consisting of a smaller element enclosed by posteriorlaterally directed rami, or the presence or absence of the more primitive single form, whether or not divided by a straight transverse suture, is usually considered sufficiently diagnostic in the instance of fossil carapaces to determine genus and establish phylogenetic relationships (e.g. see Crumly 1984; Pritchard 1979; Loveridge & Williams 1957; Schleich 1984 etc).

Most authorities have advanced the opinion that the single or transversely separated twin suprapygal should be considered a primitive form, or plesiomorphic character, (in that they more closely follow that of generalised emydids), and that the 'enclosed' form should be considered an advanced feature; the present author concurs with this view which finds support in that one of the most primitive extant forms, the rare asiatic *Manouria impressa* (GUNTHER 1882) possesses a keystone shaped transversely sutured suprapygal in combination with a hexagonal neural series.

However, even in the case of a generally accepted single genus there are often specific differences in suprapygal structure.

Testudo hermanni GMELIN 1789 has in the authors experience typically a single (keystone shaped) undivided suprapygal, and this tortoise is often regarded (with *Testudo horsfieldi* GRAY 1887) as a primitive member of the genus; *Testudo ibera* PALLAS 1814 also typically tends to feature a single suprapygal, although divided examples are also encountered⁽⁴⁾; Both forms however conform to the technical definition of the genus as a whole described above and as presently accepted by most authorities.

Supracaudal division

Reliance upon the division of the supracaudal scute as a diagnostic character should be regarded with some caution (Highfield, 1990).

Costal scute dimensions

Geochelone is differentiated from *Testudo* by the third costal scute being equal to or greater in length on its outside (marginal contact) edge than the fourth; in *Testudo*, by contrast, the order is supposedly reversed, the fourth costal being *subequal* to the third (Loveridge & Williams 1957., Pritchard 1979).

This deserves brief comment, as upon checking my own records of costal scute

⁽⁴⁾ Typically, the suprapygal division in *T. ibera* (where it occurs) is in the form of a straight or 'W' shaped transverse suture; the author has however examined one abnormal specimen from Turkey with a *diagonal* suture. A single *T. hermanni* featured a (posteriorly open) curved suture.

dimensions, I find that of 84 *T. hermanni boettgeri* for which data exists, without exception in every case the fourth costal outer suture is at least equal to and in the vast majority of cases wider than the third. If *T. hermanni* is to be considered *Testudo*, then this character cannot be used to separate *Testudo* from *Geochelone*. This same character state was also noted on the (admittedly limited) number of *T. horsfieldi* available to me. The single *T. zarudnyi* for which I have data possesses a 'standard' *Testudo* construction as do all of the (several hundred) *T. ibera* specimens for which I have records. The few *T. marginata* I have recorded also possess the typical *Testudo* pattern. See my reservations on the status of *T. hermanni* and *T. horsfieldi* (below). Of other African genera for which I have data, in *Kinixys belliana* the fourth costal is typically wider than the third; although this has much to do with the uniquely kinetic carapace found in this genus.

Costal-marginal contacts

Bour (1989) points out that in *Testudo*, the 2nd costal typically contacts the 5th, 6th and 7th marginals. This condition is also present in *Malacochersus*. In *Geochelone*, contact is typically limited to the 5th and 6th marginals.

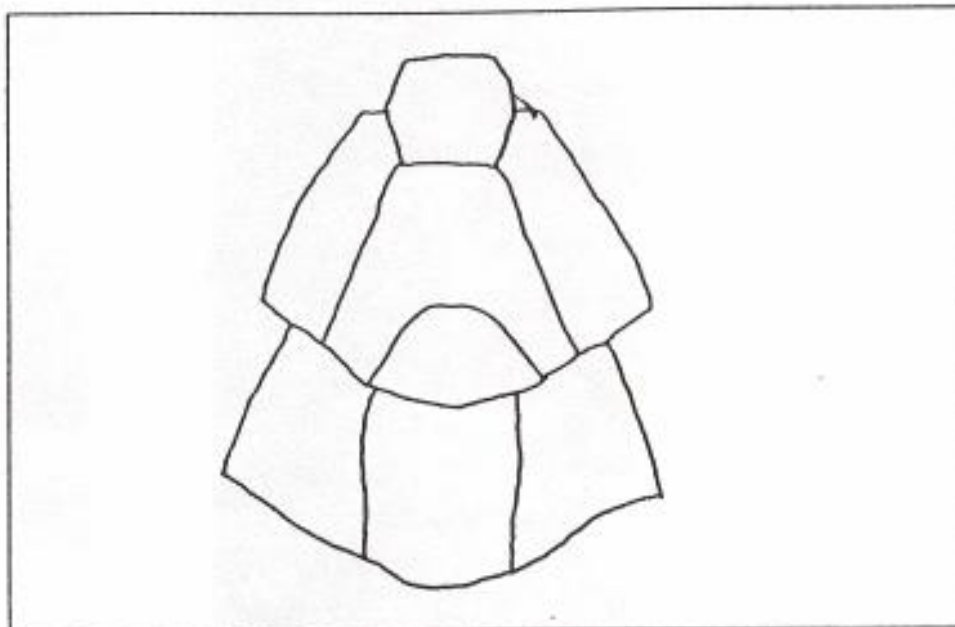
T. hermanni is again somewhat problematic with regard to costal-marginal contacts; whilst most examples maintain 5th, 6th and 7th contacts a sizable proportion (30% of *T. h. boettgeri* in my sample) do not, instead making only 5th and 6th marginal contacts. The few *T. horsfieldi* examined to date demonstrate all three contacts.

Marginal scute morphology

The sequence of reduction in the marginal scutes can provide useful diagnostic information (the marginal formula); in skeletal material this is usually discernible via the scute sulci. The position of the marginal series lateral ridge is also diagnostic in many instances.

Table 1. Typical egg dimensions of some tortoises

Species	Typical length	Typical width
<i>Testudo ibera</i>	36.00mm	30.00mm
<i>T. h. hermanni</i>	29.75mm	24.00mm
<i>T. h. boettgeri</i>	40.00mm	29.25mm
<i>F. whitei</i>	33.00mm	27.50mm
<i>T. g. graeca</i>	30.00mm	27.50mm
<i>T. kleinmanni</i>	29.00mm	23.00mm
<i>F. nabeulensis</i>	15.00mm	13.00mm



Above: Typical suprapygal of *F. nabeulensis*

Table of characters usually considered primitive

Interval between ventral processes of the prefrontals only moderately widened.*	Suprapygal single, anterior to 5th vertebral-supracaudal sulcus.**
Maxilla with triturating surface ridged, but premaxilla unridged.*	Entoplastron anterior to humeropectoral sulcus.**
Anterior palatine foramina small, concealed.*	Digital phalangeal formula 2, 3, 3, 3, 3.
Temporal arcade strong.*	Gular only slightly produced or thickened.**
Prootic well exposed dorsally.*	Gular short, broader than long.**
Quadrate not enclosing stapes.*	Epiplastron not or only slightly excavated.**
Surangular subequal in height to prearticular.*	Bridge peripherals dorsally expanded.**
4th Cervical centrum biconvex.	* Cranial character
Anterior neurals hexagonal.**	** Carapace character

Xiphiplastral kinesis

It is generally stated that whereas *Geochelone* does not demonstrate xiphiplastral kinesis, *Testudo* does - at least in females, where the character is often said to be sexually dimorphic. Whilst it is true that xiphiplastral kinesis is not present in *Geochelone*, it can hardly be described as consistently present in *Testudo hermanni*. I have in my possession a large number of *T. hermanni* carapaces and within *T. hermanni boettgeri* (of both sexes) the xiphiplastra exhibit absolutely no degree of movement whatsoever. The same observation has been made on living specimens, where they are every bit as immobile as those of *G. pardalis* or *T. horsfieldi*.

This conclusion is shared by Devaux (1988) who has very extensive experience of the southern French population of *hermanni*;

"Certaines tortues ont des plastrons articulés. La tortue grecque dispose par exemple d'une partie légèrement mobile à l'arrière. La tortue d'Hermann, au contraire, a un plastron entièrement fixe et rigide".

An identical opinion was expressed by Olivier (1894) who also commented upon the lack of articulation in *T. hermanni* compared to *T. graeca* but perhaps due to this authors confusing usage of synonyms (he habitually employed '*T. graeca*' for *T. hermanni* and '*T. mauritanica*' for *T. graeca*) his perfectly valid observations appear to have been overlooked.

On this evidence, the inclusion of the character as a definitive feature diagnostic of genus or as a key to determine sexual polarity appears seriously flawed.

On a practical note, it appears that at least one function of xiphiplastral kinesis is protection; when stimulated from behind, tortoises with this ability rapidly draw the rear lobe of the plastron upwards thereby offering improved protection to the legs and tail area. This is best observed on *T. graeca*, *F. whitei* and our Tunisian specimens where the degree of movement is considerable (in both sexes). Plastral mobility is also of obvious benefit in small species in respect of egg laying.

It must be remembered that Loveridge and Williams (1957) cite plastral mobility as a key diagnostic feature for the genus *Testudo*. In addition, plastral mobility is also absent in *Testudo horsfieldi*; a character which until quite recently was considered evidence that they belong to a different genus *Agrionemys* (Khozatsky & Mlynarski, 1966). In fact, it has been suggested that both *T. hermanni* and *T. horsfieldi* may share a common ancestry in the asiatic Oligocene-Pliocene genus *Protestudo* (see Chkhikvadze, 1970 & 1971); a hypothesis which I do not necessarily view with antipathy. Certainly, despite acknowledging that there are indeed many character states shared by *hermanni* and *horsfieldi*, and together (both cranial and carapacial) shared with *T. ibera* and *T. zarudnyi*, I confess to not being completely satisfied with their current taxonomic position and am of the general opinion that much more systematic research needs to be undertaken to resolve the many outstanding questions relating to their phylogeny. The issue of their lack of xiphiplastral kinesis is particularly problematic.

Comparative morphology of the neural series

The neural series are also extremely useful comparative characters, the ancestral hexagonal emydine pattern being replaced by alternately quadrilateral and octagonal

arrangements in more developed forms. Of extant southern African forms, *Homopus* has attained a unique semi-developed state in that it has departed somewhat from the primitive hexagonal pattern, being based upon hexagonal and quadrilateral elements (but none octagonal) and combines this with suprapygal elements which Loveridge and Williams (1957) describe as being in an incipient stage of the advanced (*i.e.* *Geochelone*) pattern from which it differs in that the sulcus of the 5th vertebral and supracaudal does not cross the middle of the second (enclosed) suprapygal element. This latter feature is also relevant to the specimens to be described in this paper from n. Africa.

External morphology of the 1st vertebral scute

The shape of the first vertebral scute, which can generally be classified as 'rounded' or 'angular' has proved to be an extremely useful and highly reliable diagnostic character (Highfield & Martin, 1989). In particular, this character can be used to differentiate with a high degree of accuracy n. European and Eurasian forms such as *Testudo ibera* and *T. hermanni* from most forms of n. African origin such as *T. graeca* and *F. whitei*. European and Eurasian forms typically possess a more or less angular frontal vertebral scute whilst *T. graeca* and *F. whitei* typically feature a rounded form (Table 2). It is our experience that typically the sulcus of the 1st vertebral scute is very sharply defined on the underlying bony tissue and this can provide useful data even in the absence of the actual scute.

The present author was struck by the complete dissimilarity between the shape of this scute in *T. graeca* from that observed in European and Eurasian forms (to which *T. graeca* supposedly bore a sub-specific relationship) and the marked similarity between that of *T. graeca* and the form observed in certain other African forms particularly *Geochelone pardalis*.

Gular morphology

The gular region of tortoises is of considerable interest and can provide very good diagnostic data. Obviously, the most distinct forms are those encountered in *Gopherus* (*Xerobates*) spp., in *Astrochelys yniphora* or in *Chersina angulata* where the projection is developed to a very high degree.

However, the gular region and associated epiplastron is generally distinctive in most groups and can provide a number of clues of considerable phylogenetic value.

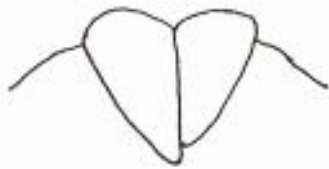
Significantly, the gular scute width of the Tunisian specimens examined typically was greater than the length; very much so in some individual specimens.

The gular scutes in many specimens were quite unlike anything ever observed in any *Testudo* species; one was immediately reminded instead of *Homopus* and *Malacochersus*. In a high percentage of specimens, the gular scutes extended across the entirety of the anterior epiplastron (fig. 5) being extremely wide and narrow.

This character state is quite remarkable, and is entirely inconsistent with that found in *T. hermanni*, *T. ibera* and other circum-mediterranean species in my experience. We found this state in two very young juveniles, several sub-adults and also adults of obvious maturity. So it is not an ontogenetic effect. When plastral photographs are compared with *Testudo* specimens, the difference is immediate and striking.

Table 2 Comparative 1st vertebral scute characteristics

Species	Description
<i>T. hermanni</i>	Typically very angular.
<i>T. ibera</i>	Typically very angular to moderately angular. Regional variations.
<i>T. g. graeca</i>	Rounded, typically somewhat indented anterior lower quarter.
<i>F. whitei</i>	Very rounded. anterior indents slight or entirely absent.
<i>G. pardalis</i>	Typically angular, some lateral convexity.
<i>F. nabeulensis</i>	Typically somewhat angular, lateral edges often somewhat convex.



1. *T. graeca*

2. *F. nabeulensis*



3. *Homopus*



4. *Malacochersus*

Fig. 5 Gular morphology

Gular rise and excavation

Also very notable was the degree of gular rise above the plastron; in many cases the angle of rise was very acute, the anterior epiplastra being markedly convex and in all cases was considerably in excess of that which one is accustomed to observing in circum-mediterranean species.

Internally, the degree of excavation of the gular and epiplastron may be considered an indication of a derived or primitive condition; *Manouria impressa* (on the basis of the 3 carapaces available to us) entirely lacks excavation, *Manouria phayrie* is also ill-developed and in *T. hermanni* the degree of epiplastral excavation is also usually severely restricted; in *T. ibera* and most n. African specimens examined by us, as well as in most *Geochelone* specimens, internal epiplastral excavation is typically well developed.

Humeropectoral sulcus

The position of the humeropectoral sulcus in relation to the entoplastron is significant. In *T. hermanni* and in *Indotestudo* the sulcus typically crosses the entoplastron. In *Geochelone*, *T. ibera* and n. African tortoises the sulcus is typically located posteriorly and exteriorly to the entoplastron. In some tortoises (e.g. *Manouria impressa*) the humeropectoral sulcus typically coincides with, but does not significantly cross, the posterior suture of the entoplastron-hyoplastron.

Cranial osteology

Cranial characters are extremely important and valuable diagnostically, and have been discussed in considerable depth by Gaffney (1979), Crumly (1982) and with regard to *Testudo* by Bour (1989) among other commentators. Cranial characters are however not analysed in any detail in this present paper in connection with the specimens described as further work on these is in progress; it is a complex subject which requires detailed discussion and it is intended to produce a separate paper illustrating and describing their characters at a later date. Certain cranial characters must be referred to, albeit only generally in our present context.

Prootic shape and exposure

The shape and percentage of dorsal exposure of the prootics (which are penetrated by the *stapedial foramen*) are determined by the overlap of the parietals; this is however a character which to a greater or lesser extent is affected by the overall size of the cranium. Small specimens typically showing less prootic exposure than large specimens. In large specimens (e.g. *Geochelone [Aldabrachelys] gigantea*, *G. [Chelonoidis] elephantopus* etc.) the anterior prootics may be revealed with a different shape to the posterior prootics, a feature which is clearly of diagnostic value. Most species of *Geochelone* have prootics which are narrow throughout their length or wider posteriorly than anteriorly (Crumly, 1982).

The degree of dorsal prootic exposure is particularly important since it is one of the principal characters employed by Loveridge & Williams (1957) to differentiate between *Geochelone* and *Testudo*. These authors considered the character so important that they italicised it in their diagnostic criteria for *Testudo* outlined on page 254; "*prootic typically concealed dorsally and anteriorly by parietal*". However, the same authors (on page 218) previously state "*prootic completely concealed by the parietal*" (my italics). There is an obvious difference between "completely concealed" and "typically concealed". Bour (1989)

prefers to employ the term 'reduced' compared to *Geochelone* rather than concealed.

Smaller genera typically exhibit much less of the prootic dorsally than do inherently larger genera; however, there are exceptions in that *Malacochersus*, for example, reveals a relatively high percentage of prootic for its size.

Triturating surface of the maxillary

This character is employed frequently to diagnose *Geochelone*, although Bour (1989) has also pointed out specific differences between *T. graeca*, *T. (graeca) ibera*, *T. marginata*, *T. kleinmanni*, *T. hermanni* and *T. horsfieldi*. There tends to be an inherent difference between large and small tortoises. In African genera, the triturating surface of the maxilla in *G. pardalis* is particularly serrated.

Supranasal squamation

Loveridge & Williams (1957) cite the presence of supranasal scales as co-diagnostic for *Testudo* and point out that these are also present in *Malacochersus*; they are absent in *Geochelone*.

Distribution

Until very recently the universally accepted distribution of *Testudo* in north Africa was that *Testudo graeca* LINNAEUS 1758 occurred throughout Morocco, throughout Algeria, into Tunisia and extended to Libya where it eventually connected with *Testudo kleinmanni* which then replaced it. One single report of *Testudo graeca* exists for Egypt (quoted in Lambert, 1983) although as no description or illustration is provided for this creature it is impossible to determine precisely what it was; obviously it was something other than *T. kleinmanni* but on our evidence, we doubt that it was indeed a true *T. graeca* but rather some externally similar Libyan form as yet unclassified. There is also always the possibility of an introduced specimen (*see below*); this grim spectre, which was surely sent specifically to haunt taxonomists, is also discussed by Loveridge & Williams (1957). My own experience of Libyan tortoises however suggests that there are indeed some which externally and superficially at least resemble *T. graeca*, but which on close (osteological) examination feature character states which conclusively separate them, e.g a *Geochelone-Homopus* type suprapygal. For a review and illustrations of some Libyan tortoises see Schleich (1989).

Introductions

The natural European distribution for *T. graeca* L. 1758 is limited to a relatively small population in Southern Spain (Lopez Jurado *et al.*, 1979) although secondary populations are also reported from Mallorca - certainly in the early 1980's pet shops in Palma were selling *T. graeca* shipped from southern Spain and one faunal checklist implies that *T. graeca* is extinct on the island (Kramer & Vickers, 1983). Some *T. graeca* from the Rif in Morocco were also deliberately introduced to the Coto Donana nature reserve in SW Spain (Valverde, 1960). Other reports indicate small populations of alleged introduced *T. graeca* in southern Italy, and on the islands of Sardinia and Sicily (Bruno 1970; Bruno and Maugeri, 1976). The present author has been fortunate enough to examine closely a specimen of alleged *T. g. graeca* from Sardinia and can state with confidence that it is not a *T. graeca* L. 1758 at all but is instead one of the much larger Algerian species with the remarkable suprapygal construction to be described. Apparently Sardinia was a popular place to release tortoises as various dislocated oddities have been recorded from there including alleged *T.*

marginata (Bruno and Maugeri, 1976; Hellmich, 1962). Although this latter reference may actually concern large Algerian derived specimens which have a long history of being mistaken for *T. marginata* on account of their pronounced posterior marginal lateral extension (e.g., see Strauch 1862).

The Mertens hypothesis

Within *Testudo graeca* L. 1758 Mertens (1946) alleged four sub-specific forms; the evidence presented for this however is poor, and is in one case based upon a single preserved specimen (*Testudo zarudnyi* NIKOLSKI 1896) and in another instance upon no specimen at all (or even an illustration of one) and an admitted complete lack of any personal knowledge of the alleged animal (*Testudo floweri* BODENHEIMER 1935). This latter attribution was revised in 1958 to *Testudo graeca terrestris* FORSKAL 1775 by Wermuth who concluded that the mysterious *floweri* form was identical to two specimens examined by himself; one from Syria and one from Derna in Libya. Unfortunately, neither of these specimens appears valid as Forskals '*terrestris*' and the status of any nomenclatural act by Forskal is also highly questionable in this particular instance for reasons discussed at length in a paper shortly to be published (Highfield & Martin, in press). The entire sub-species hypothesis as proposed by Mertens for *T. graeca* is not accepted by the present author. Some reasons for this are discussed in a previous paper (Highfield & Martin, 1989). Suffice to say, Mertens found "only relatively minor differences in shell proportions" between n. African and Caucasian '*T. graeca*'. A somewhat surprising conclusion in view of the true level of divergence and range of sizes which actually does exist between the populations. At the same time, it is necessary to recognise that Mertens based his conclusions upon only a small handful of specimens - and his observation that n. African tortoises "maximum size...is set at 250mm" also suggests that he was unfamiliar with all of the available literature concerning this subject. 250mm is in fact the standard or average SCL of female *F. whitei* from Algeria, many specimens attaining 280mm and one 30 year old specimen in our own collection measures 292mm. Mertens erroneously considered Bennetts' *T. whitei* a mere synonym of Moroccan *T. g. graeca*. It is interesting to note that using similar criteria Mertens also concluded that all U.S gopher tortoises (*Xerobates* spp.) were mere subspecies and not full species. This conclusion (unlike his *Testudo* conclusions) never gained acceptance.

Taking the African continent as a whole, the following situation represents the generic distribution pattern as currently accepted by all known authorities (fig. 6). *Testudo* is here limited in distribution to the coastal band running from Morocco to Egypt. Some climatic and geophysical reasons for this distribution are provided by Lambert (1983). The nearest points of (extant) *Geochelone* approach are the Sudan, Mauritania, Ethiopia and Eritrea for *G. sulcata* and the Sudan, Mauritania and Ethiopia for *G. pardalis*. The closest approaches of *Kinixys* (as *K. belliana belliana*) also occur in the Sudan, Eritrea and Ethiopia. *Homopus*, *Psammobates*, *Chersina* and *Malacochersus* as genera are exclusively restricted to distribution in southern Africa. Loveridge & Williams (1957) nominated *Pseudotestudo* as a new subgenus to include *Testudo kleinmanni* LORTET 1887. Recently, however, Bour (1989) has shown that the characters supposed for this genus (quadrate not enclosing stapes) are based upon juvenile phase cranial development within *Testudo*. This tortoise should therefore continue to be regarded as a *Testudo*.

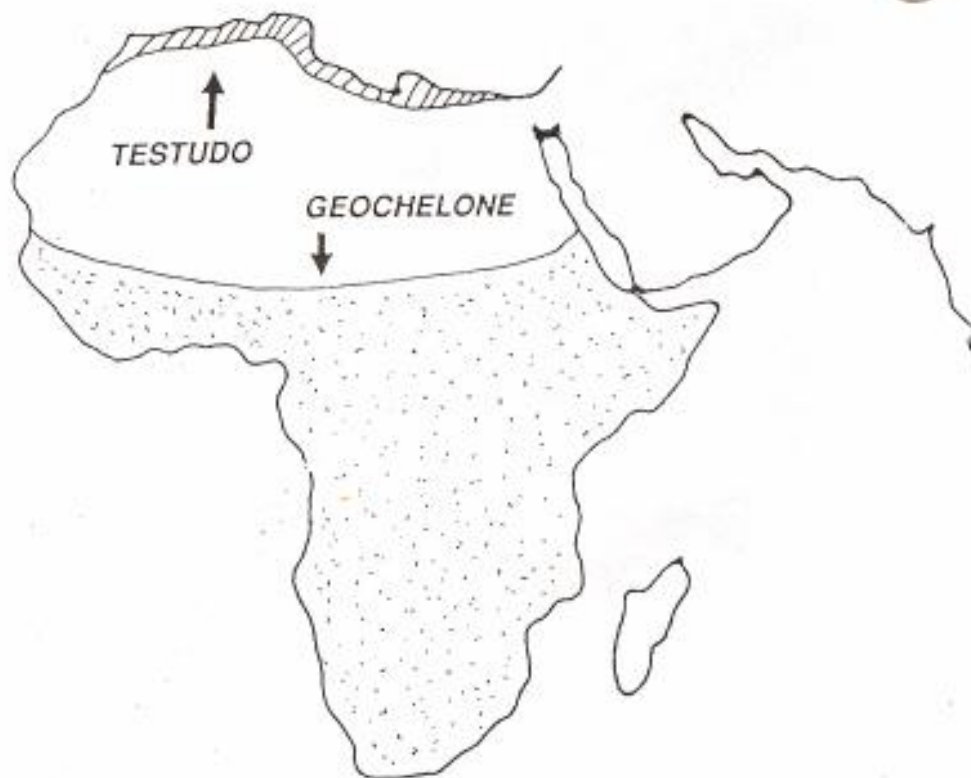


Fig. 6 Currently accepted distribution of *Testudo* & *Geochelone* in Africa

Fig. 7 Alleged sub-specific distribution of *T. graeca* (source: I.U.C.N.)



Fossil history

It is clear from fossil evidence that the distributions of these genera were once very much more extensive than today. *Geochelone* in particular was a very successful and widely distributed genus. *Testudo* was similarly widely distributed with extensive fossil evidence from Europe especially. Of *Homopus* we unfortunately know much less due to the extreme paucity of specimens (of any age).

For a general overview of fossil land tortoises see Auffenberg (1974), Crumly (1984), Mlynarski (1969 & 1976), Meylan & Auffenberg (1986) and Gaffney (1979). Some interesting hypotheses upon the distribution of fossil tortoises associated with changes in past climates derived from paleobotanical data are presented by Brattstrom (1961) who also provides a series of very useful maps covering periods from the Cretaceous and Eocene to the Pliocene and Recent.

Some specifically north African fossil forms are discussed by Dacque (1912), Bergounioux and Crouzel (1968) and by Bergounioux (1952 & 1954-55) who in the latter publication described *Testudo semenensis* from Djebel Semene in Tunisia.

Unfortunately, very little fossil material from north Africa has ever been collected and classified; for obvious reasons, chelonian material from what is now the Sahara desert is virtually non-existent. *Our knowledge of the evolution of land tortoises in north Africa is therefore extremely poor.*

Much of what has been accepted has been done so on the basis of assumption and speculation rather than on the basis of any physical evidence which in most cases is entirely lacking. Indeed, most of these tortoises have never been systematically studied in modern times using current technology.

The view that *Testudo*, and only *Testudo* remains the only extant living genus in the region has not, however been seriously challenged until now; the only exception to this being the erection of *Pseudotestudo* by Loveridge & Williams (1957), a conclusion and nomenclatural act now considered invalid for the reasons stated by Bour (1989) and with which the present author concurs fully.

North Africa; A tortoise Galapagos of the Mediterranean?

If what all known authorities currently state to be true actually is true, then one would not expect to find tremendous divergence among the tortoises of the region; those of Morocco should not differ greatly from those of, for example, Tunisia, Algeria or Libya; and there should definitely be no major and consistent structural divergence from the criteria accepted for the genus as a whole, or indeed between any series of n. African specimens and a similar series of, for example, *Testudo (graeca) ibera* PALLAS from Europe.

Let us address this question directly. In Algeria there exists a tortoise which habitually attains quite tremendous dimensions. The largest (female) example seen by the author measured 292mm in straight line carapace length and weighed some 4,550g (Highfield, 1990 and in press). This tortoise (of which I have had the opportunity of examining very many similar specimens both alive and prepared) conforms to the type specimen of *F. whitei* (BENNETT 1836). Some details of this species have been presented earlier (Highfield & Martin, 1989). This same animal lays eggs which typically measure some 33mm long x 27.5mm wide. The resulting hatchlings measure some 33mm in length.

In Tunisia, by contrast, exists at least one population of tortoises which even as fully grown (female) adults reach a maximum straight line carapace length of some 150mm and which typically weigh less than 750g. These animals lay eggs which typically measure a tiny 15mm long X 13mm wide.

By almost every criteria it is possible to devise, these animals are entirely and consistently different from one another; size; markings; colour; carapace shape; cranial shape; egg size; hatchling size and internally they differ in osteological structure. Yet for 250 years they have generally been regarded as not only the same species, but since Mertens' paper of 1946 as the same sub-species 1. If these are indeed to be regarded as the same species, then what of the status of Galapagos tortoises or even of Darwins' famous finches? In the latter case, identification is said to be difficult even for an expert ornithologist in some instances, so slight are the external signs of divergence and speciation (Jackson, 1985).

Furthermore, these are not the only forms which exist in the region which fail entirely to conform to diagnostic criteria for the species said to be in exclusive occupation, namely *Testudo graeca* LINNAEUS 1758.

Let us now turn to some of those specimens; these should demonstrate a limited range of divergence, and should without question conform to the criteria already outlined above for *Testudo graeca* specifically and for *Testudo* as a genus.

They manifestly do not.

Comparison should in all cases be made to the Holotype of *Testudo graeca* as described below.

***Testudo graeca* LINNAEUS 1758 - the holotype**

The holotype of *Testudo graeca* LINNAEUS 1758 is founded upon the illustration which appeared on page 204 of George Edwards' *Natural History of Birds* published in London 10 years previously (see also Bour, 1987).

The figure "represents it of its natural bigness" and depicts a well drawn and accurate carapace measuring 104mm in length and 64mm in height. The head, legs and tail were not available to the artist and these leave something to be desired in the way of accuracy, being more representative of a lizard than a tortoise. The plate is hand coloured and shows a small tortoise having a general yellow groundcolour with dark brown to black markings.

Of this specimen Edwards writes;

"I had the male and female of this species; they lived two years with me, in the garden of the College of Physicians, London. In the warm months they copulated by leaping, in the common way of most four-footed animals. I was in hopes of propagating the species, but could never see any of their eggs in the places where they scraped holes.

The iris of the eye was of a reddish hazel-colour; the lips were hard, like the bill of a bird. the head was covered with scales of a yellowish colour; the neck, hinder legs and tail were covered with a flexible skin of a dirty flesh colour that they might be the more pliable to be put forth and drawn into the shell. The fore-legs were covered with yellow scales on their outsides which are partly exposed when the legs are drawn in. The shell is round, and pretty much rising on its upper side, and flat underneath; it is

divided into many compartments, or separate scales, which have furrows or creases all round them, lessening one within another to the middle part of each scale. The shell is of a yellowish colour, clouded and spotted with large and small irregular spots of dusky or black; the vent is in the tail itself, which the female turns up in coition, and the male turns his tail inward under it, which brings the vents of each to touch. It hath five claws on each foot forwards, and four on each of the hinder feet. When they apprehend danger, they draw the head, tail and legs into the shell so that they cannot be easily hurt.

This tortoise was sent to me from Santa Cruz in West Barbary by my late friend Mr. Thomas Rawlings, Merchant, who died there (Anno 1748) after some years settlement in that country".

Type Locality

The locality of "Santa Cruz in West Barbary" refers to the old fort of Santa Cruz located on a hill close to the city of Oran, Algeria.

Nomenclature

In the main heading opposite the illustration the animal is referred to simply as 'The African Land Tortoise'; later it appears as *Testudo tessellata africana minor* (nomen nudum). It received the name *Testudo graeca* in the 10th edition of the *Systema Naturae* of 1758.

Of the name *Testudo graeca* applied by Linnaeus to a tortoise exclusively from Africa, Statius Muller (1774) explains;

"The Mosaic tortoise, *Testudo graeca*. The artistic placing of various coloured stones into shapes is called mosaic or musaic work and this art came from Greece to Italy 500 years ago. If one now perceives that the shell of this variety of tortoise is covered almost exclusively with square 'leaves', which have a number of hollows in the squares, making even smaller squares, one will immediately realise the origin of the name 'Greek' or 'Mosaic' tortoise".

Synonymy

The synonymy of *Testudo graeca* is extensive, but perhaps the best known synonym is *Testudo mauritanica* DUMERIL & BIBRON 1835.

Dimensions & probable age of the specimen

At 104mm this is undoubtedly a young specimen. The average adult size of male tortoises examined by the author from northern Morocco and the region of Oran is 145mm. This figure agrees closely with that of Lambert (1982) who studied tortoises in the same region. Annual growth lines are clearly visible in Edwards illustration and vary between 9 and 13 in number on the various scutes; from this, we can infer that the animal was probably approximately 10-12 years of age. The latter growth lines are fairly wide and all appear well defined. In aged specimens this is not so. The attained length of 104mm would also be consistent with an estimated age of 10-12 years in this species. Sexual activity can certainly occur at 7-8 years of age, so again this tends to confirm an age of circa 10 years for Edwards specimen.

Carapace height & curvature

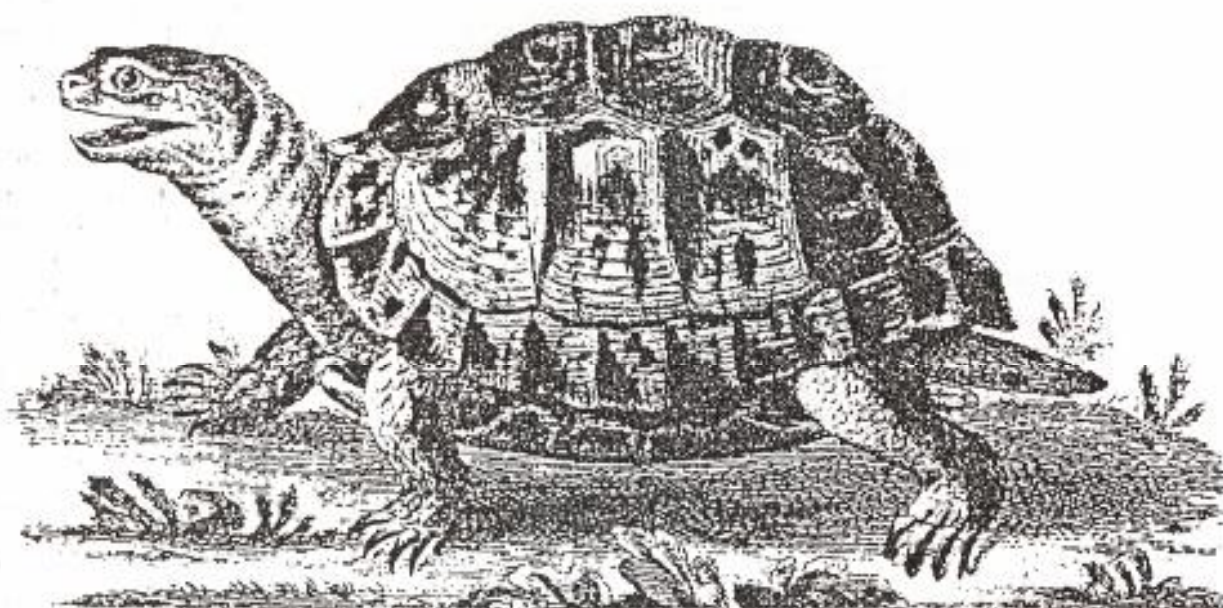
Measured from the illustration this is revealed as 64mm, producing a height/length ratio of 1.64 - entirely consistent with young male *T. graeca* from the same locality today (typical adult male ratio range 1.70 - 1.85).

Variation of colour & morphology within *T. graeca*

Gross variations within the true species from the region of the type locality have not been frequently encountered - most individuals conforming quite closely to the holotype in colouration, markings and overall morphology. Some darker individuals are encountered (especially in the north of Morocco), and in some specimens the marginal 'saw-tooth' or 'V' markings are more or less defined. However, in the principal specific characters comprising the unique frontal vertebral scute, adult length and body mass range no significant deviations have been noted in confirmed specimens from the type locality. A typical *T. graeca* L. 1758 from Oran is shown in plate 1. This should be compared directly to the holotype illustrated in fig. 9.

The holotype of *T. graeca* when studied closely is revealing; it depicts a tortoise bearing characters which place it firmly from the stated type locality and which can be seen, in identical form, in tortoises from that particular locality today. What is significant is that these characters seem restricted to a population of fairly limited distribution and are not seen in other specimens from different localities in north Africa.

Fig. 9 *T. graeca* L. 1758 (ex-Edwards, 1748)



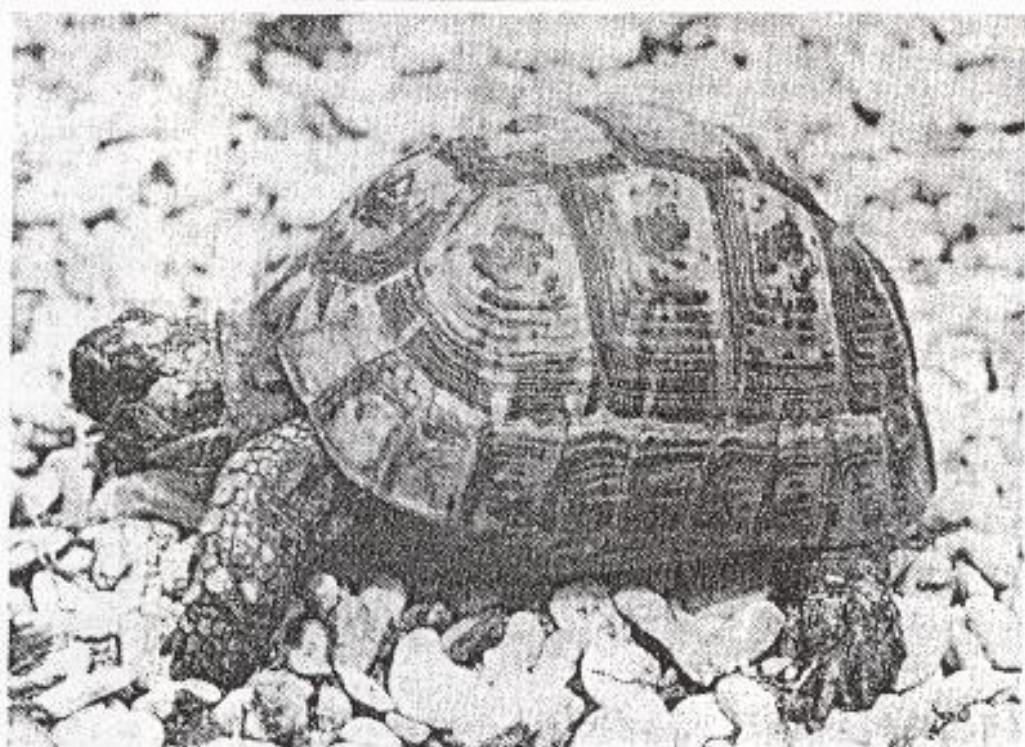
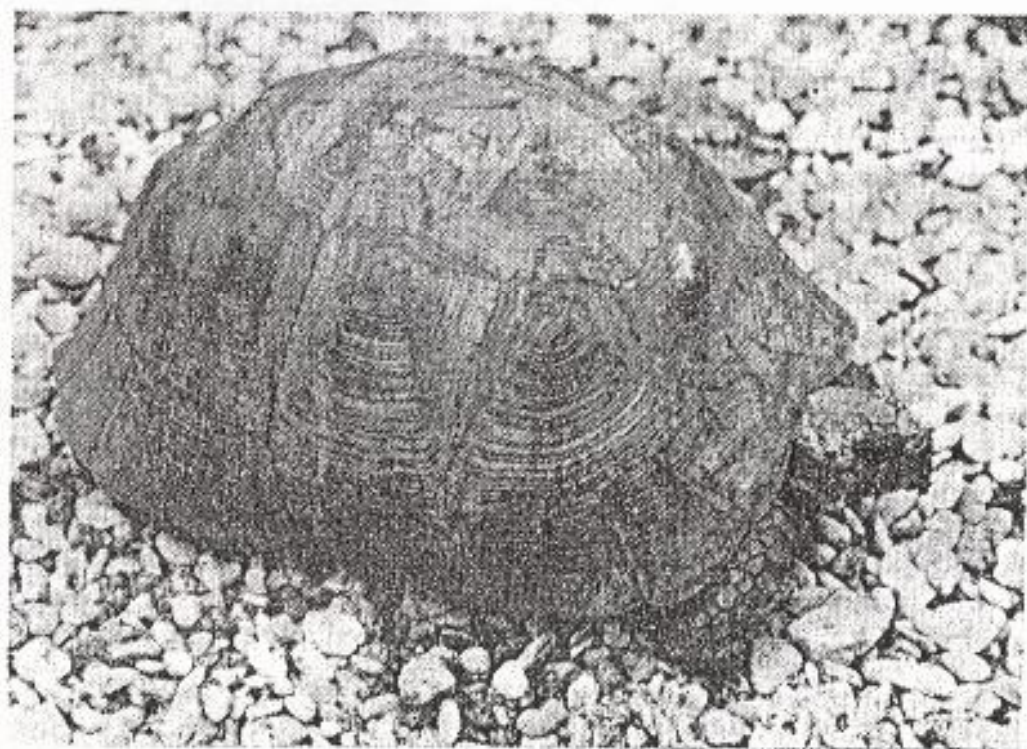


Plate 1 (above). *T. graeca* L. 1758 from Oran, Algeria

Plate 2 (below). *F. whitei* BENNETT 1836 from Algiers, Algeria.



Osteological analysis of a *T. graeca* specimen

To enable comparison with other n. African specimens to be described, data is here presented obtained from a carapace from the extreme east of Morocco (bordering Algeria). This tortoise was a very elderly male which died from natural causes associated with old age. The carapace was preserved intact apart from the xiphiplastron which was lost.

SCL:-	140.00mm
Plastron length:-	N/A
Carapace height:-	72.00mm
MwM:-	103.00mm
Fw:-	89.0mm
LoC:-	191.00mm
Epiplastral excavation:-	YES
Gular length:-	21.75mm
Gular width:-	22.75mm
Gulars enter entoplastron:-	(8.00mm)
Gular height:-	13.25mm
Skeletal mass:-	180g (without xiphiplastron)
PaG:-	N/A
Anal notch width:-	N/A
Epiplastron midline length:-	12.00mm
Entoplastron midline length:-	21.50mm
Hyoplastron midline length:-	22.00mm
Hypoplastron midline length:-	30.50mm
Xiphiplastron midline length:-	N/A
Average marginal series width:-	16.61mm

Description:- There are 9 pairs of pleurals and 11 pairs of peripherals; there are 3 major pleural-peripheral suture contacts, the 5-6, 8-9 and 10-11 peripheral sutures contacting the 3-4, 5-6 and 7-8 pleural sutures; The marginal lateral ridge is very weak; the marginal scute sulci reduce in a series from 1>2>11>10>9>3>8>4=5=6=7 (21.50mm, 20.50mm, 20.00mm, 19.50mm, 18.25mm, 16.00mm, 15.00mm and 4 X 13.00mm) a total marginal series length of 182.75mm and an average of 16.61mm; there are 9 neurals configured 4-8-4-8-4-8-4-5-4; the suprapygal is 2-piece, separated by a single straight suture; the pygal is oblong and measures 25mm by 20mm; the nuchal bone (proneural) attains a maximum width of 37mm

narrowing to 21.50mm at its anterior edge; the outer edge of the 3rd costal scute sulcus measures 37.25mm and that of the 4th measures 29.50mm, thus in this example the 4th is greater than the 3rd; the 1st costal contacts the 1st, 2nd, 3rd, 4th and 5th marginals, the 2nd contacts the 5th, 6th and 7th marginals, the 3rd costal contacts the 7th, 8th and 9th marginals and the 4th costal contacts the 9th, 10th and 11th sulci of the marginal series; the supracaudal is not much posteriorly projected and is but little introflexed ventrally; the 5th vertebral extends somewhat downwards towards the suprapygals below the general line of the costal-marginal seam; the humero-pectoral sulcus does not cross the entoplastron, but passes it anteriorly (by 5mm).

Remarks:- This specimen typifies the problems facing the chelonian taxonomist; in several ways it demonstrates gross individual variety and abnormality, most notably in the number of pleurals and the posterior configuration of the neurals. Whilst neural variants are quite commonly encountered, it is extremely unusual to find an additional pair of pleurals - which in this instance are located posteriorly and are immediately adjacent to the suprapygals. Also non-typical in this specimen are the lateral ratios of the 3rd and 4th costal scutes.

The most important point to be considered at all times during osteological analysis of chelonians is that a wide range of inconsistency and variability *even within what are sometimes regarded as 'fixed' diagnostic characters* occurs with disturbing frequency. This same point was emphasised by Loveridge and Williams (1957) who state that;

"At every point in our taxonomic study we have been faced with the fact that in all characters the amount of variation exhibited by members of this order is frequently astonishing.....this high degree of variability extends to osteology also.....*the only certain test of stability (is the) empirical one of examining a large series*".

This approach is undoubtedly the correct one, and is the method adopted during this current study. Without exception, I have always insisted upon examining a series of specimens before reaching any conclusions in respect of the range of normality for the race, species or genus. *It is, in my view, extremely foolhardy and dangerous when working with chelonians to erect new taxa upon single specimens which may or may not be typical of their supposed grouping.*

This necessity to base all conclusions upon carefully collated data from a series cannot be stressed to highly; it is absolutely vital. Not only preserved specimens must be examined, but that data must be compared to living specimens both in captivity and in their natural habitats. This presents obvious difficulties (some tortoises are extremely rare and some habitats are highly inaccessible). However, it is the ideal towards which we should aspire.

In every case where I have suggested the erection of new taxa, or the modification of previously classified groupings I have done so *without exception upon the basis of a study of as large a series in each case as possible*. In all cases, at least 6 specimens of each type have now been analysed in detail, and in most cases data from between 20-50 individual specimens has been studied.

Where an individual specimen to be described deviates from the normal structure of the group to which it is assigned, this is remarked upon as in the case of the *T. graeca* described above. Although that specimen does demonstrate quite extreme variation in some quite major characters (neural series, costal dimensions and pleural series) it is nonetheless

still regarded by me as a *T. graeca* - although not as a particularly typical one with regard to these specific character states. Overall however, it satisfies me that it is correctly referred on the general balance of character states.

Radical deviations do exist and are found in some individual specimens from time to time, but these do not diminish the phyletic value of the categories whose definitions they transgress. It is the stability of series which carries weight, and the balance of characters within individuals which determines referral. High-level characters such as overall pygal region or cranial structure naturally carrying more phylogenetic weighting than lower level characters such as external markings or squamation where variability is often extreme.

Proposed new genera from north Africa

1. *Furculachelys nabeulensis* nov. gen, nov. sp.

Carapace morphology	Holotype	Topotype
SCL:-	121.00mm	120.00mm
Plastron length:-	111.00mm	N/A
Carapace height:-	64.50mm	62.00mm
MwM:-	88.50mm	93.00mm
Mw:-	85.00mm	86.50mm
Fw:-	78.00mm	80.00mm
LoC:-	155.00mm	160.00mm
Epiplastral excavation:-	YES	YES
Gular length:-	18.50mm	18.00mm
Gular width:-	24.50mm	22.00mm
Gulars enter entoplastron:-	(6.00mm)	(7.00mm)
Gular height:-	15.50mm	15.50mm
Skeletal mass:-	112.00g	110.00g
PaG:-	22.75mm	N/A
Anal notch width:-	28.50mm	N/A
Epiplastron midline length:-	8.00mm	8.50mm
Entoplastron midline length:-	19.50mm	21.00mm
Hyoplastron midline length:-	15.00mm	17.00mm
Hypoplastron midline length:-	24.50mm	24.00mm
Xiphiplastron midline length:-	25.50mm	N/A
Average marginal series width:-	14.14mm	14.59mm

Topotype: An adult male from the Tunisian coastal zone, precise locality unknown due to the specimen having being subject to transportation. For general characters see description of Holotype, from which it differs only in possessing an additional suture in the 1st suprapygal. No other significant variation from the Holotype, other than purely allometric deviations are evident. The xiphiplastron of this specimen is missing.

Holotype: An adult male, found lying on its back dead in a forested area in the region of Nabeul, Tunisia in April 1990 by Miss M. Hill. Most body tissue had decayed, and there was evidence of rodent attack, the anterior part of the skull having been consumed. The carapace remained intact with the exception of a displaced pygal (which was found nearby and subsequently restored to the carapace) and the 2nd suprapygal element which is still missing. However, as the 1st suprapygal and pygal are both present, the shape and size of this are evident.

Descriptions and comparisons: This is an intriguing and highly interesting specimen. The carapace is very well preserved and fortunately we also have a large mass of data from living specimens from the same locality with which to compare it; this leaves no doubt that it is a very representative sample and is in no way abnormal for the locality (which in this instance may be interpreted as the Tunisian coastal zone generally).

There are 8 pairs of pleurals, and 11 pairs of peripherals. The sulci of the marginal scutes in each case cross the peripheral bones at the midline between sutures with a slight posteriorly directed inclination, and the 3-4, 6-7 and 7-8 peripheral sutures make perfect contact with the 1-2, 3-4 and 5-6 pleural sutures respectively; a total of 3 lateral peripheral-pleural contacts. There is only a very weak lateral ridge to the marginals with 75% above and 25% below.

The marginal scutes reduce in a series (measured at their outer edge) from $2>1>9>10>4=11=8>5>6=7$ (19mm, 18mm, 17mm, 15mm, [13mm x 3], 12.5mm [11.5mm x 2]), a total marginal series width of 155.50mm. If this figure is divided by 11 the result is an average marginal series width of 14.14mm. The AMSW is a very useful guide figure, being both dimorphic and, when combined with the marginal formula, specifically diagnostic.

The 7 neurals are configured 4-8-4-8-4-8-6, the latter element contacting the anterior edge of the 1st suprapygal. The suprapygal itself consists of two elements (the second missing) the former bifurcating posteriorly in the form of two rami which enclose the smaller secondary element. The sulcus of the supracaudal-fifth vertebral scute does not cross the suture of the pygal and 2nd suprapygal but coincides precisely. The pygal is a straight oblong, convex on its outer face and somewhat introflexed on its ventral face measuring 19.75mm x 15mm with a maximum tissue thickness of 6.75mm. The nuchal bone measures 17mm wide at its anterior edge, and attains a maximum width of 31mm. It measures 15mm deep. The outer edge of the 3rd costal scute-marginal contact sulcus measures 23mm and that of the 4th 20mm. Thus the 4th is subequal to the 3rd. The outer sulcus of the 2nd costal contacts the 5th, 6th and 7th marginal sulci, the 1st costal contacts the 1st, 2nd, 3rd, 4th and 5th marginal sulci, the 3rd costal contacts the 7th, 8th and 9th marginal sulci and the 4th costal contacts the 9th, 10th and 11th marginal scutes.

The posterior suture of the entoplastron contacts the humeropectoral sulcus, but is not actually crossed by it; the entoplastron is entered by the posterior component of the gular sulci. The small inguinal scutes do not obviously contact the femoral scutes.

The gular region is paired, thickened and anteriorly terminates simultaneously on a plane with the nuchal zone, not projecting at all beyond it; internally, the epiplastron is quite substantially excavated.

The bridge peripherals are not significantly expanded dorsally and there is but a weak lateral ridge. This character is powerful in primitive tortoises (e.g. *Manouria*) and its reduction is considered derived. Of southern African genera, *Homopus* and *Psammobates* both possess a significant lateral ridge combined with unexpanded bridge peripherals.

Remarks: This carapace is conclusively and absolutely separated from *Testudo* by the bifurcating suprapygals which in many respects approaches that of *Homopus*; it differs from *Homopus* however by the possession of a series of octagonal-quadrilateral neurals. It is also separated from *Geochelone* by possessing a xiphiplastral hinge. The sulcus of the supracaudal and 5th vertebral intersects at the exterior suture of the suprapygals and pygal; a character state not present in post-Eocene forms of *Geochelone*. Further, the degree of rise or curvature on the anterior face of the 2nd (enclosed) suprapygals is quite extreme and definitely closer to that seen in *Homopus* than in *Geochelone* (especially the extant s. African *G. pardalis*); it is, in fact, closer to an inverted 'V' shape rather than a simple arc of a circle. Another character state inconsistent with either *Testudo* or *Geochelone* is that the gulars are paired, but typically very profoundly broader than long not only in the Type Specimen but also throughout the general population of the Type Locality, sometimes extremely so, in a manner again very reminiscent of *Homopus*.

Unfortunately, only a relatively small skull fragment survives, but from this it is obvious that the parietals almost completely obscure the prootics; the species is therefore defined upon the small adult body size as described above, and the genus upon the following principle combination of character states; the mobile xiphiplastron; the gulars typically wider than long; the two or three-part suprapygals, the outer larger element bifurcating posteriorly to embrace the second, smaller element which rises approximately to or just above the midline of the first; the first element having no transverse divisions or one single transverse division located above the anterior suture of the 2nd (enclosed) element; typically the epiplastron rising on its anterior face and internally excavated below the introverted gular lip.

Etymology: The generic name *Furculachelys* is derived from *Furcula* (Latin = forked) and *Chelys* (Latin = tortoise) indicating the principal diagnostic condition of the suprapygals. The specific name *nabeulensis* refers to the *terra typica* of Nabeul, Tunisia.

Living appearance: In life, these tortoises are very brightly coloured with a yellow groundcolour featuring black markings; the vertebral scutes feature a black central blotch, anteriorly and laterally bordered by a brown-black band. The costal scutes typically feature a centralised black dot, more or less enlarged or distinct, in some specimens surrounded by additional irregular small black dots or blotches; the 2nd, 3rd and 4th costals are typically bordered anteriorly and at the marginal contact with bands of black, but the 1st costal typically lacks the anterior border at the 1st vertebral contact. The marginals are typically bordered anteriorly with a moderately narrow black band at each contact; in some specimens this marking is more extensive, becoming almost triangular; in yet other specimens, the marginals feature a series of lateral dots rather than any anterior borders. The plastron normally features a large central diffuse black marking centered upon the abdominal region.

The markings of hatchlings are similar, but typically the groundcolour is a paler shade of

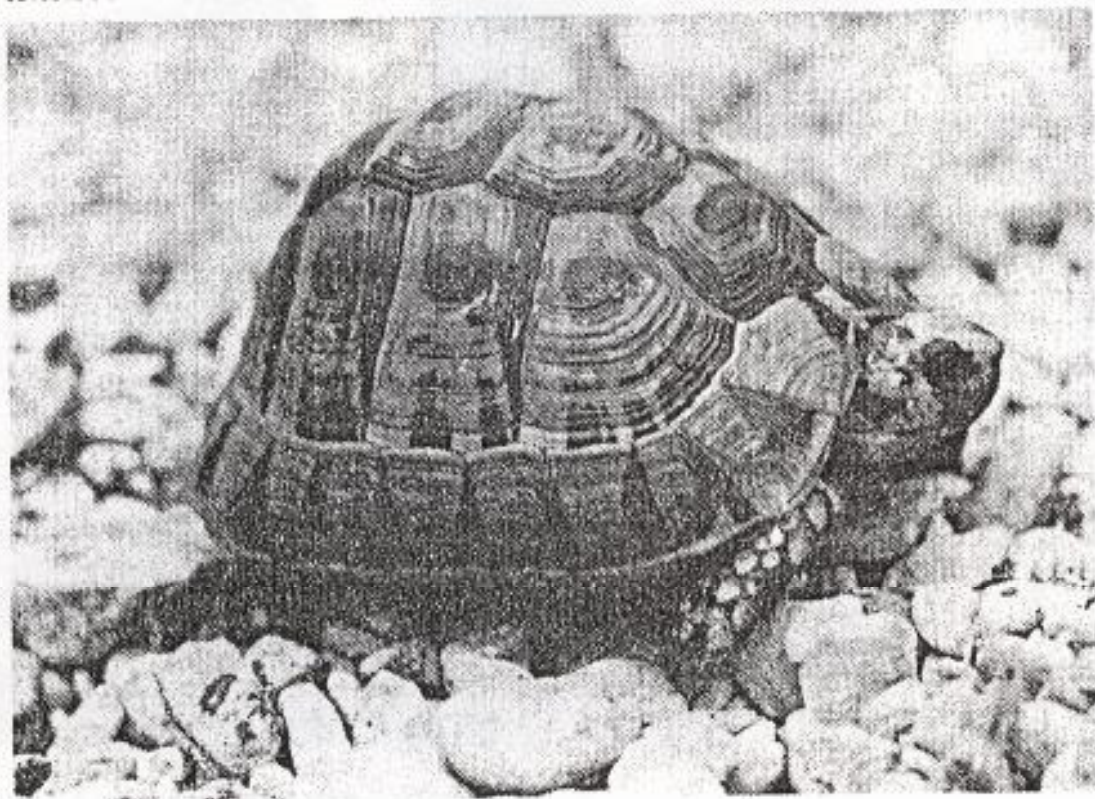
yellow and the carapace markings tend to be browner, rather than pure black.

There are very noticeable regional variations in marking; even some neighboring populations each possessing distinct variations upon the basic pattern. In one instance, we found two populations separated by only a few kilometers which each bore striking individual characteristics. Interestingly, every tortoise examined within those populations bore the same 'local' marking, but each population was very different from the other.

The scales of the front legs are typically light or sandy yellow, sometimes tipped with black; the skin itself is usually sandy yellow. Dorsally, the head is usually centrally marked with a large yellow blotch which may be more or less distinct. There are typically two bright yellow supranasal scales. The hind legs may feature large spike-like scales, typically yellow in colouration, at or about the heels. There are small thigh tubercles present, occasionally paired.

The eyes are small, very black and bright. When captured, female specimens often retreat into their shells and peer tentatively out, but male specimens show a remarkable lack of fear, waving their front legs wildly in anger and frustration, and when finally released, make their escape into the nearest cover at a remarkably high speed. Two males placed together will immediately begin to fight, circling for advantage with much butting and some occasional biting.

For additional data on *Furculachelys nabeulensis*, see the earlier comments on these tortoises in the same authors 'Preliminary Report' (Highfield, 1990).



Furculachelys nabeulensis

***Furculachelys whitei* (BENNETT 1836)**

Carapace morphology	Topotype
SCL:-	262.00mm
Plastron length:-	225.00mm
Carapace height:-	120.00mm
MwM:-	173.00mm
Mw:-	177.00mm
Fw:-	149.00mm
LoC:-	345.00mm
Epiplastral excavation:-	Yes
Gular length:-	36.00mm
Gular width:-	40.00mm
Gulars enter entoplastron:-	Yes (11mm)
Gular height:-	24.00mm
Skeletal mass:-	870g
PaG:-	38.00mm
Anal notch width:-	48.00mm
Epiplastron midline length:-	25.00mm
Entoplastron midline length:-	37.50mm
Hyoplastron midline length:-	37.50mm
Hypoplastron midline length:-	56.00mm
Xiphiplastron midline length:-	51.00mm
Average marginal series width:-	31.59mm

Descriptions and comparisons: This is but one of a series of similar specimens from the Algiers region of Algeria studied by the author. Data is now held on file for several prepared carapaces and in excess of 35 living specimens, both male and female. Annual growth data for some individual specimens is available over 18 years. These tortoises belong to the same genus and species as described by Flower (1945) under the synonym *Testudo graeca graeca*, and are the same tortoise described in a preliminary paper by the present author under the nomenclature *Testudo whitei* BENNETT 1836, or "Gilbert White's Tortoise" (Highfield and Martin, 1989).

At the time that preliminary paper was published, osteological work had not commenced

for a lack of skeletal material. Fortunately, adequate material to permit such a study has now been located and the conclusion reached then on the basis of external characters that these tortoises are not in fact *T. graeca* L. 1758 but a totally different animal (which had been described as such in 1836 by E. T. Bennett in a footnote to an edition of White's 'Natural History of Selborne') is now confirmed by analysis of the internal osteological characters. The first carapace, described above, was prepared by Indrani Das, for whom recognition is hereby extended for first noting the unique suprapygial structure and drawing that to the present authors attention. Subsequently, I have prepared additional carapaces from donated pathological material and a good deal of osteological data on this taxon has now been accumulated.

The following remarks and observations apply strictly to the female carapace figured and described above (males are somewhat smaller).

There are 8 pairs of pleurals and 11 pairs of peripherals. There is but a single direct peripheral-pleural vertical suture contact, at the 1st pleural and 3-4 peripheral. In all other cases, the coincidence is off-set. There is but a moderate lateral ridge to the bridge peripherals; stronger than that typical of *T. graeca*, but less than typical of *Manouria* or *Homopus*.

The marginal scutes reduce in a series from 2>1>11>9>6>7>8=10>5>4>3 (38mm, 36mm, 35mm, 34mm, 33mm, 31mm, 30mm x 2, 29mm, 27mm and 24mm), a total marginal series length of 347.50mm and an average marginal series ratio of 31.59.

The neurals are of particular interest. They are configured (anteriorly to posteriorly) 5-5-9-4-8-4-8-6 a total of 8. Their number and structure are really very unusual but are by no means unique in this tortoise generally - although not every specimen possesses an identical sequence. The most distinctive features are undoubtedly the two small pentagonal, but elongate, anterior elements and the 3rd 9 sided element. Nothing approaching this arrangement typically exists in either *Testudo* or *Geochelone*, for which Loveridge and Williams (1957) state;

"Typically the anterior neurals alternately octagonal and quadrilateral"

It is important not to infer too much from a single neural series as this character state is subject to variability in a percentage of individuals (Lydekker, 1889; Hay, 1908; Auffenberg, 1976). It would certainly therefore not be advisable to base a taxon upon a single such example or even the minority percentage of a series. As stated, whilst this particular specimens neural series is unusual, it is not unique. A more typical arrangement in whitei however would feature a series of 6-8-4-8-4-8-6 sided elements.

The suprapygial consist of three elements; the uppermost element begins as 50% of a hexagon, in a mirror image of the final neural (at which the vertebrae terminate), but then at its mid-line, terminates in an almost perfect 'W' shaped suture which connects it to the second element, which in turn, fully encloses a third.

The 2nd element features two posteriorlaterally bifurcating rami which enclose the 3rd and final element which is convex on its superior aspect, the ventral aspect remaining as an open arc of a circle.

This character is typical of the taxon as a whole (confirmed by serial studies) although some examples demonstrate a sharper rise to the anterior face of the last element, closer to

that of *Homopus* or that previously described as typical of *Furculachelys nabeulensis*. In addition the 2nd suprapygal element is single or fused in some individuals, i.e it lacks the 'W' shaped transverse suture.

The sulcus of the 5th vertebral scute and supracaudal coincides with the suture of the pygal and 3rd suprapygal element but does not cross it (as it would in post-Eocene *Geochelone*).

This sulcus is not straight, as is usual in mediterranean tortoises such as *T. marginata*, *T. ibera*, *T. hoisfieldi* and *T. hermanni*, but is instead extended ventrally in the region of the pygal. Something very similar is seen in southern African *G. pardalis*, in *Aldabrachelys gigantea* and in other *Geochelone* species examined by the author; although in such cases the sulcus is not coincidental with the suture. This arrangement would appear to be fairly typical of all n. African tortoises generally (including *T. graeca* and *T. flavominimalis*) but is atypical in european or asian species.

The pygal itself is oblong and measures 36.50mm long by 28.50mm wide. It has a maximum tissue thickness of 11.25mm.

The nuchal (proneural) bone measures 41.50mm wide at its anterior edge and attains a maximum width of 56mm at the 1st marginal-pleural juncture. It is 45mm long, the superior aspect being somewhat recessed to accommodate the anterior terminal of the pentagonal 1st neural.

The outer edge of the 3rd costal-marginal scute contact measures 60mm and that of the 4th measures 49mm. The 4th being subequal to the 3rd. The outer sulcus of the 2nd costal contacts the 5th and 6th marginal scutes but not the 7th, the 1st costal contacts the 1st, 2nd, 3rd, 4th and 5th marginals, the 3rd costal contacts the 7th, 8th and 9th marginal sulci, and the 4th costal contacts the 9th, 10th and 11th marginal sulci.

The posterior suture of the entoplastron does not contact the humeropectoral sulcus, but passes above it (anteriorly) by some 5mm. The entoplastron is entered somewhat by the gular sulci. The inguinal scutes do not obviously contact the femoral scutes. The gular region features two paired scutes, is thickened upon its superior face, but does not rise significantly; in fact, the gular lip is somewhat introflexed exteriorly in a ventral direction. Internally, the epiplastron is quite substantially excavated. The superior frontal aspect of the gular lip is not much rounded (as it is in *F. nabeulensis*) but instead is flattish and in lateral view inclines downwards at a sharp angle; it is quite long from front to back, 31.50mm in this specimen.

The xiphiplastra are mobile in both sexes.

Remarks: These tortoises are among the largest of all mediterranean land tortoises, and are very close indeed to *T. marginata* in overall dimensions; so much so that they have regularly been mistaken for that species (as indeed was the holotype of *Testudo whitei* by no lesser authorities than Gray and Bell). Not only do they attain similar dimensions, but they also possess very significant posterior marginal scute serrations - in many cases, these equal those of genuine *marginata*. As with *marginata*, these serrations are not present in hatchlings and juveniles, but they do begin to manifest with adulthood. By maturity, the serrations are very evident. It is not true however to say that they indicate "very old"

specimens (Boulenger, 1891). They are fully developed by 20-25 years of age, by which time a typical female can already measure over 260mm long (SCL) and weigh in excess of 3,500g. No matter what age true *T. g. graeca* L. attain (based upon study of those from the actual type locality), they never reach anything even approaching these dimensions nor do they develop the extreme posterior marginal serrations so typical of Algerian *whitei*.

Adult males of this species are typically smaller than adult females, but still very much larger than male *T. graeca*, *T. hermanni* or *T. ibera*. I recently measured three adult male *F. whitei* from Algeria with the following results;

SCL	LoC	Ch	Weight
-----	-----	----	--------

260mm	350mm	120mm	3,200g
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250mm	320mm	118mm	2,750g
-------	-------	-------	--------

240mm	295mm	111mm	2,350g
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These are very remarkable dimensions - especially when compared to typical adult male weight and length data taken from *T. g. graeca*. The largest male recorded above (260mm SCL) was evidently of considerable age judged by carapace condition, but the other two specimens were of no more than moderate age.

Osteologically, these are a heavily built and robust tortoise very similar in many ways (particularly in lateral profile) to *G. pardalis*, though they have much reduced maximum dimensions (circa 300mm to 600mm for *pardalis*). Length for length, their body mass is also significantly less than an equivalent length *G. pardalis* as their carapace is nowhere near so domed, being very broad and flat by comparison - e.g I recently weighed a 290mm female *whitei* at 4,650g and a 300mm female *G. pardalis* at 8,900g.

Although is not intended to detail cranial characters in this present paper, it is worth noting the following general (preliminary) observations made from a skull derived from a 250mm (SCL) female *F. whitei*;

Length = 40mm; internal quadrate separation = 21mm; median minimum frontal width = 9.50mm; the prootics well concealed anteriorly in dorsal view.

Compared to a *T. g. graeca* skull, the most immediately striking difference is to be seen at the posterior aspect of the parietal where the flat and angular first section of the supraoccipital compares to the gently downwards directed curve of the *T. g. graeca*. The supraoccipital itself is long and its dorsal edge is very straight. The triturating surfaces of the maxilla are more strongly ridged in *whitei* than in *graeca*, and the interprefrontal space is not so narrowed ventrally in *whitei* as in *graeca*; in fact, the typical state in *F. whitei* is that it actually expands somewhat laterally as it contacts the palatal arch externally; on the lower jaw, the coronoid processes of *graeca* are typically raised to a point, whereas in *whitei* these are typically rather flattened and suppressed.

Further details of the cranial characters of *F. whitei* will be published separately.

specimens (Boulenger, 1891). They are fully developed by 20-25 years of age, by which time a typical female can already measure over 260mm long (SCL) and weigh in excess of 3,500g. No matter what age true *T. g. graeca* L. attain (based upon study of those from the actual type locality), they never reach anything even approaching these dimensions nor do they develop the extreme posterior marginal serrations so typical of Algerian *whitei*.

Adult males of this species are typically smaller than adult females, but still very much larger than male *T. graeca*, *T. hermanni* or *T. ibera*. I recently measured three adult male *F. whitei* from Algeria with the following results;

SCL	LoC	Ch	Weight
-----	-----	----	--------

260mm	350mm	120mm	3,200g
-------	-------	-------	--------

250mm	320mm	118mm	2,750g
-------	-------	-------	--------

240mm	295mm	111mm	2,350g
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These are very remarkable dimensions - especially when compared to typical adult male weight and length data taken from *T. g. graeca*. The largest male recorded above (260mm SCL) was evidently of considerable age judged by carapace condition, but the other two specimens were of no more than moderate age.

Osteologically, these are a heavily built and robust tortoise very similar in many ways (particularly in lateral profile) to *G. pardalis*, though they have much reduced maximum dimensions (circa 300mm to 600mm for *pardalis*). Length for length, their body mass is also significantly less than an equivalent length *G. pardalis* as their carapace is nowhere near so domed, being very broad and flat by comparison - e.g I recently weighed a 290mm female *whitei* at 4,650g and a 300mm female *G. pardalis* at 8,900g.

Although is not intended to detail cranial characters in this present paper, it is worth noting the following general (preliminary) observations made from a skull derived from a 250mm (SCL) female *F. whitei*;

Length = 40mm; internal quadrate separation = 21mm; median minimum frontal width = 9.50mm; the prootics well concealed anteriorly in dorsal view.

Compared to a *T. g. graeca* skull, the most immediately striking difference is to be seen at the posterior aspect of the parietal where the flat and angular first section of the supraoccipital compares to the gently downwards directed curve of the *T. g. graeca*. The supraoccipital itself is long and its dorsal edge is very straight. The triturating surfaces of the maxilla are more strongly ridged in *whitei* than in *graeca*, and the interprefrontal space is not so narrowed ventrally in *whitei* as in *graeca*; in fact, the typical state in *F. whitei* is that it actually expands somewhat laterally as it contacts the palatal arch externally; on the lower jaw, the coronoid processes of *graeca* are typically raised to a point, whereas in *whitei* these are typically rather flattened and suppressed.

Further details of the cranial characters of *F. whitei* will be published separately.

Etymology: This tortoise was named after the naturalist Gilbert White. It was originally regarded as belonging to *Testudo*, and should now be referred to *Furculachelys*.

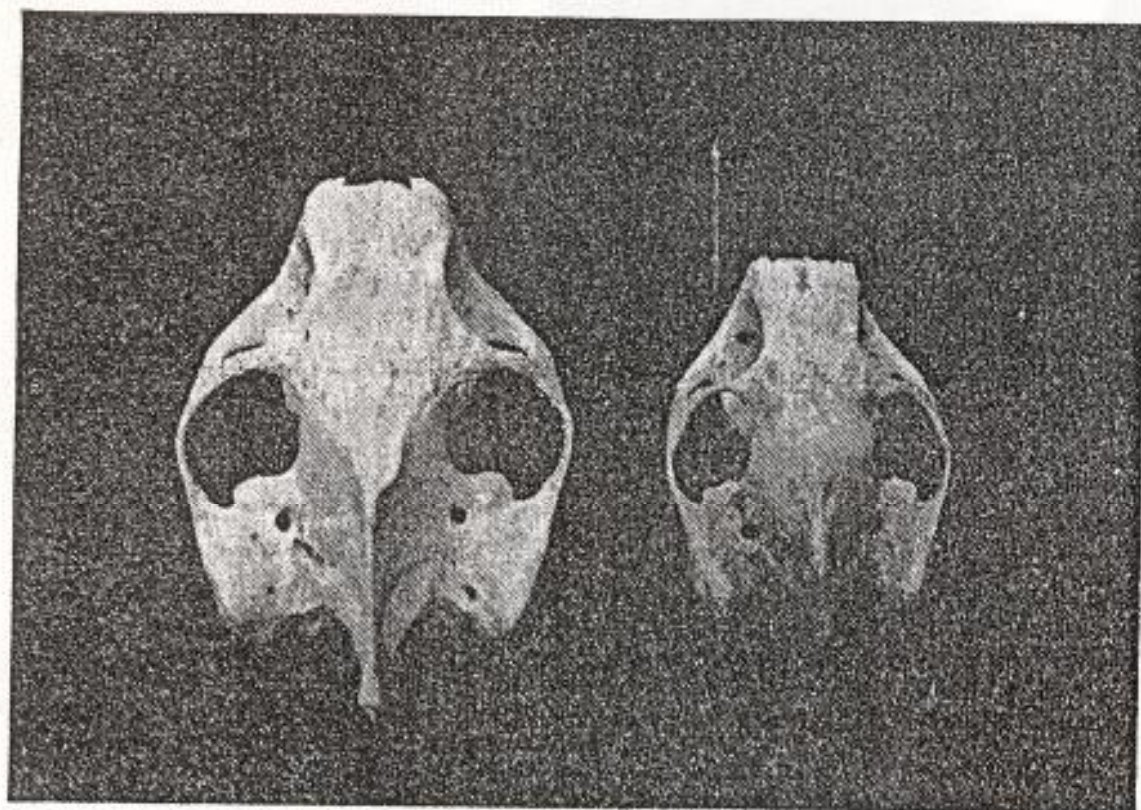
Living appearance: The most striking externally visible difference between *T. graeca* and *F. whitei* (apart from their sheer size) is that *F. whitei* entirely lack the central black dot and border vertebral-costal scute patterning. In *F. whitei*, this is replaced by an often spectacularly beautiful medullary ray pattern. I have seen no *F. whitei* with a dot and border pattern. Typically, the groundcolour is a golden yellow but may tend towards a brownish yellow on some examples.

The forelegs feature large imbricate scales and the head is often yellowish. The thighs feature extremely large laterally intumed spurs very similar to those seen on *G. pardalis*. These spurs are not rudimentary, as seen in *T. graeca*, but are very enlarged and are typically ivory or whitish in colour.

The largest (female) specimen encountered to date measured 292mm SCL and weighed 4,550g. This specimen was of known age (30 years). Quite a number of specimens have been measured with a SCL in excess of 280mm. Most females however measure circa 250-275mm SCL and weigh between 3,000-3,500g. Males are somewhat smaller and typically measure between 215-240mm SCL and weigh between 2,000-2,500g. Data for three males of exceptional size was presented above.

Hatchlings typically measure some 33-34mm long and eggs measure (on average) 33mm long x 27.50mm in width. Average clutch sizes = 8-12, exceptionally as many as 16.

Below: cranium of *F. whitei* (left) & *T. graeca* (right)



***Testudo flavominimmaralis* HIGHFIELD & MARTIN 1989**

Carapace morphology	Holotype
SCL:-	133.00mm
Plastron length:-	118.00mm
Carapace height:-	64.75mm
MwM:-	97.00mm
Mw:-	90.00mm
Fw:-	80.00mm
LoC:-	163.00mm
Epiplastral excavation:-	Yes
Gular length:-	19.00mm
Gular width:-	25.00mm
Gulars enter entoplastron:-	Yes
Gular height:-	15.00mm
Skeletal mass:-	180g
PaG:-	20.00mm
Anal notch width:-	28.25mm
Epiplastron midline length:-	9.00mm
Entoplastron midline length:-	20.00mm
Hyoplastron midline length:-	11.00mm
Hypoplastron midline length:-	30.00mm
Xiphiplastron midline length:-	27.50mm
Average marginal series width:-	16.04mm

Holotype: An adult male of considerable age. Scutes still present, removed on one side for the purposes of this study. Type Locality = Libya.

Descriptions and comparisons; Although this is a small carapace compared to *F. whitei* and even to *T. graeca*, it is actually quite a large representative of its species. Most male specimens are on average some 15-20mm less in SCL than this example. For males, a typical SCL would be between 110-120mm. This particular specimen is very old, the carapace demonstrating many of the signs typical of extreme ageing including extensive surface erosion. The tortoise was known to have survived in captivity for some 25 years after importation from Libya during which time little if any growth was recorded.

There are 8 pairs of pleurals and 11 pairs of peripherals. There is extensive erosion in the marginal region which makes precise measurement and examination difficult, however, there appears to be but one pleural-peripheral vertical suture contact at the 5-6 pleurals and the 7-8 peripherals.

The marginal lateral ridge is very slight, almost absent. The 7 neurals are perfectly configured 4-8-4-8-4-8-6 the latter element contacting the suprapygal which is of typical *Testudo* pattern in that it comprises two elements divided by a single straight transverse suture. The pygal is oblong and measures 19.50mm long by 17.00mm wide. It attains a maximum bone tissue thickness of 6.00mm. Unlike the pygal area of *F. nabeulensis*, the pygal and supracaudal zone of *T. flavominimmaralis* is not at all projected posteriorlaterally and is not introflexed ventrally; in fact, although this is a male specimen, the supracaudal is less developed or projected than a typical female *F. nabeulensis*. The outer face of the pygal is gently convex.

The 1st costal scute measures 40.50mm wide at its outer edge, the 2nd measures 26mm, the 3rd also measures 26mm and the 4th measures 28mm, therefore the 3rd costal is sub-equal to the 4th. The nuchal bone (proneural) measures 21mm long by 33mm wide. The nuchal scute itself is long (13mm) and narrow (4mm).

The marginal scutes measure, from front to back, 21mm, 20mm, 16.50mm, 14mm, 14mm, 13mm, 12.50mm, 14mm, 17mm, 18mm and 16.50mm a total marginal series length of 176.50mm.

The first costal scute contacts the 1st through 5th marginals, the 2nd costal contacts the 5th, 6th and 7th marginals, the 3rd costal the 7th, 8th and 9th marginals, and the 4th costal scute contacts the 9th, 10th and 11th marginals.

Cranial osteology: The skull is remarkably small and fragile, measuring but 29mm long. The quadrates are separated (internally) by 15mm, and the transverse frontal width is 6.75mm at its narrowest point. The prootics are almost fully exposed posteriorly and quite well exposed anteriorly. Typical comparative measurements for *T. g. graeca*; length = 31.75mm, quadrate separation = 18mm, transverse minimum frontal width = 7.25mm.

There are however, other differences of cranial form which are best illustrated rather than described; these include a very much greater angle of lateral divergence in the quadrates of *T. flavominimmaralis* compared to *T. g. graeca*, and the presence of a severe anteriorlaterally and ventrally directed slope or angle to the dorsal surface of the quadrates.

Additionally, the anterior aspect of the quadratojugal in lateral view is less curved in *T. flavominimmaralis* than in *T. g. graeca*. Also in *flavominimmaralis* the anterior aspect of the premaxilla appears considerably projected compared with *T. g. graeca* although this is mainly due to a lateral reduction in the anterior face of the maxilla. Posteriorventrally, the maxillary process is less sharply angular and projected in *T. flavominimmaralis* than in *T. g. graeca*, and the jugal is but little excavated or contoured posteriorly. The palatine-vomer ridge is stronger and sharper in *T. flavominimmaralis*, and the entire palatine area is much more arched and angular than is typical of *T. g. graeca*.

This tortoise was first described by the above authors in 1989 on the basis of external morphology and the following notes on those characters are herein repeated;

Carapace markings:

Groundcolour bright yellow, dark brown to black central dot on vertebral and costal scutes which are edged in black, marginals marked with indistinct brown-black dots, the 'V' or 'Saw-tooth' pattern characteristic of *T. graeca* L. is absent or ill defined, the yellow groundcolour of the vertebrals, costals and marginals frequently features a random distribution of smaller black dots and flecks.

Skin and scale colouration:

The skin of the shoulders and thighs is typically orange-yellow and may feature darker brown-black flecks, the skin of the neck and scales of the head are typically very bright yellow, in the case of the head often giving the appearance of a mask. There is typically a large bright yellow frontal scale on the top of the head. The scales of the anterior limbs are bright yellow and black.

Plastron markings:

The plastron is typically of a somewhat duller yellow-amber colour than the carapace and features an expanse of brown-black marking in the region of the abdominal and femoral scutes or a more diffuse series of brown-black blotches.

These tortoises are somewhat enigmatic in that they appear to have entirely escaped previous description despite there being numbers of them held in captivity. One reason seems to be the confusion associated with Wermuth's alleged '*Testudo graeca terrestris*' - certainly, I have encountered owners of these little tortoises who seemed to think that they were in possession of a '*terrestris*'. In fact, these tortoises bear no resemblance whatsoever to any alleged '*terrestris*' save for the light yellow head colouration, a character typical of various n. African species including *F. nabeulensis* and many individual *F. whitei*. It is worth noting that these are exclusively north African tortoises, and that they are not found in the region where Forskal allegedly described *Testudo terrestris* in 1775 (Lebanon/Syria). They are also very much smaller than the tortoise of that region, which express a very close phenetic relationship to *Testudo ibera* PALLAS 1814 rather than to any n. African form.

An excellent colour plate featuring *T. flavominimaralis* appeared under the synonym *Testudo graeca terrestris* in a colour poster published and distributed by Zoo-Med Laboratories Inc. of California ('Turtles of the World' poster # P102, 1987).

I have examined a number of males of this species, but only two females which seem to be very rare.

Details of eggs and hatchlings are presently unknown.

Etymology: The specific name is derived from *Flavo* (Latin = yellow) and *minima* (Latin = miniature).

Tortoises, species and endemism; discussion, problems and a hypothesis

Endemic taxa at all levels (genus, species or sub-species) are those which are confined to a discrete geographical region. Divergence, variation and ultimately selective evolutionary developments are most likely to occur when individual populations are isolated from one another by geophysical or environmental factors which limit or prohibit genetic interchange between them. Islands are for obvious reasons the classic example of this mechanism.

However, islands do not represent the only circumstances under which this mechanism can operate; north Africa with its isolated djebels (mountains), massifs, plains, oases and hammadas is an equally stimulating environment for natural selection, adaptive evolution and divergence.

The required time-scale for such speciation to manifest however is problematic; nonetheless, it is a fact that many n. African and particularly Saharan mammals demonstrate sufficient morphological divergence throughout their geographical range to be accorded sub-specific status (Ranck, 1968).

One factor which is of critical importance in respect of tortoises is these animals already extremely limited potential for mobility. Wide ranging gene flow between isolated populations is rendered, by this factor alone, much less probable than would be the case with a more mobile animal. Tortoises also have very specific environmental requirements; to a tortoise, an exposed area offering no cover or retreat from the heat of the day is as impassable as the highest mountain. Such factors contribute to the continuing long-term isolation of individual populations. For all practical purposes, an isolated oases or hillside population of tortoises may as well be on a real island; they cannot leave their environment and no new genetic material can reach them.

Neo (1978) reports that heterozygous values generally tend to be higher in reptiles than in birds or mammals, however island populations are more generally homogenous (Frankel and Soule, 1981). Because of their highly specific biotypic requirements and generally isolated habitats with minimal transit of individuals between populations a high degree of genetic convergence is often found within groups of reptiles. Where a greater exchange of individuals occurs, in more easily traversed and larger habitat areas then a state of balanced polymorphism may occur between homozygous, dominant homozygous and recessive individuals (Croudace, 1989).

These factors may have combined to accelerate speciation and adaption within the n. African environment and to *preserve in isolation relict species*.

With respect to tortoise populations, it is worth noting the following basic criteria which tend to exist generally which prohibit interbreeding between various species;

- a) They are incompatible structurally
- b) They occupy different habitats
- c) They have different breeding times or mechanisms
- d) They are incompatible genetically

Insofar as n. African tortoise populations are concerned, it appears that all four factors are present to greater or lesser degrees.

Of the first point, structural incompatibility, it would be very difficult indeed to find a better illustration of this than is to be found in the case of *Furculachelys whitei* and the miniature tortoises (both *Testudo* and *Furculachelys*) of Tunisia and Libya. The possibility of successful mating occurring for physical reasons between these two groups has to be considered highly unlikely to say the least. A *F. whitei* male for example is on average some 350% larger by body mass than a female from Sidi Kalifa and intromission must be considered a virtual impossibility.

Of the last point, unfortunately at this stage little reliable data actually exists; however, given the range of other divergent characters present it seems no unreasonable to assume that marked genetic divergence must also exist and that it probably is sufficient to inhibit interbreeding in at least the majority of cases. Certainly, the authors own experiences in captive breeding n. African tortoises strongly suggests that unless obviously 'identical' pairs are used fertility is generally very poor. The most consistent successes obtained have been where both parents are quite clearly very convergent in all recognisable external characters. Some alleged reports of interbreeding in '*T. graeca* sub-species' are quite obviously based upon mistaken and confused identifications of the breeding pairs in the first place.

It is hoped to present additional data on this subject in a subsequent paper; however, data already collated is sufficient to demonstrate beyond all reasonable doubt that different populations produce uniquely formed eggs, have hatchlings of different size on emergence and different early phase growth rates. This is in addition to their possessing unique visible characters such as body shape or markings which are always entirely consistent with others derived from the same population, but which are often quite unlike those of neighboring populations.

One is left to speculate about where these tortoises actually came from. The hypothesis advanced by Loveridge and Williams (1957) is that;

"the separation of the African and east European races has not been of long standing, it is natural to infer that formerly a continuous population extended across southern Europe whence the invasion of Western north Africa occurred via Spain and not across Egypt. In this view, the southern Spanish population of *T. graeca* would be a relict one, persisting after the general extinction of the species in western Europe".

This assumes that Mertens was correct in his view that *Testudo ibera* PALLAS 1814 and *T. zarudnyi* NIKOLSKI 1896 were closely related sub-species of the n. African *graeca* and that it is indeed *T. graeca* L. 1758 and *T. graeca graeca* L. 1758 alone which populates the n. African coastal zone from Morocco to Libya. A view which this present paper now refutes.

It may well be necessary to consider *T. horsfieldi* and *T. hermanni* separately as despite the cranial evidence for their belonging to *Testudo* many other powerful character states tend to disassociate them.

On this topic, which cannot be discussed at length here, the evidence of Kirsche (1984) is often cited; the hybridisation of *T. horsfieldi* with *T. hermanni* does not prove that *horsfieldi* is *Testudo*, but does support a close relationship between the two. A view which I also share.

Various aspects of divergence between the African *graeca* and its alleged European sub-species have been described by other authors, most notably by Bour (1989) who

analysed cranial material and by Obst and Ambrosius (1971) who studied serological evidence. Considered with other evidence both sets of results must also call into serious question Mertens (1946) hypothesis of the sub-specific status of the European tortoises. The suprapygial evidence presented here is in any event overwhelming and conclusive; these tortoises are certainly not *Testudo graeca graeca* and cannot possibly be closely related to either *T. hermanni* or to *T. ibera*, *T. marginata* or *T. zarudnyi*.

If a close phylogenetic link between northern (*Furculachelys*) and southern African forms is hypothesised (and the suprapygial evidence in particular would strongly support this), then one does not have to look very far to find one possible reason why they are now separate; the encroachment of the Sahara within the continent.

Until only comparatively recently in evolutionary terms, large areas of what is now barren desert were lush savannah and thick forest. 1,000,000 years ago the climate of n. Africa was essentially tropical. 50,000 years ago mankind's ancestors discovered fire and began to use axes to clear the forests. 10,000 years ago the Aterian Caucasoid Proto-Hamite culture inhabited the region of Gafsa in Tunisia and extended their culture's influence (Capsian Man) as far south as Kenya - although some authorities express doubts regarding the precise chronology and extent of population in this era (Balout, 1981).

The cutting of wood for fires, the increased burden placed upon the land by grazing herds and the localised changes in the flora and climate this brought about is what made the barren Sahara we now know. These changes are advanced throughout the entire Mediterranean region (Le Houverou, 1980).

Details apart, we can be certain that as little as 5,000 years ago the Sahara was very different from today and supported a much wider and more typically southern African fauna; "the Sahara was an area with rich populations of wild animals and thriving life" (Rzoska, 1984).

A more detailed account of the creation of the Sahara, and the destruction of forest and wildlife this entailed is presented by Hugot (1974). What is clear is that the diversity of animal life present was truly remarkable, and that most of it was what we would today associate more with southern Africa rather than northern Africa; Hippo, elephant, gazelle, ostrich, lion, panther, giraffe, antelope, leopard and a host of other game. Some of these creatures were indeed only annihilated from north Africa within the last 100 years (the last lion and panther were shot in Tunisia at Babouch, near to Hammamm Bourgiba) and it was not until 1983 that the last Atlas Leopard was presumed shot in Morocco; fortunately, there remains a faint possibility that at least one small group may still survive (Haddane, 1989). Scullard (1974) points out that forest elephants grazed at the foot of the Atlas mountains as recently as 480 B.C. and occurred from the Mediterranean to the Cape of Good Hope in south Africa. The general reptile fauna of n. Africa generally has much in common with southern African species.

If this biotype was suitable for such creatures, what of its tortoises? And were they *Geochelone-Homopus* like or *Testudo* like? The only certain thing is that their bones now lie buried under the desert sands which destroyed and claimed their habitat. Many species which previously inhabited the central Sahara have become extinct since the Pleistocene. But are some of the n. African coastal tortoises of today their descendants?

Tortoises are of course widespread in southern Africa, with a rich diversity of forms (e.g.

Geochelone, *Kinixys*, *Homopus*, *Psammobates*, *Chersina* and *Malacochersus*). Some of which occur sympatrically. In north Africa only two forms, *Testudo graeca* (and that as an alleged subspecies), and a more distantly related form, *T. kleinmanni* are said to exist; a somewhat anomalous and remarkable state of affairs given the previously alluded to faunal richness of the region and its undoubted ability to support such creatures.

If one considers the now extinct general zoological fauna of the region, and the affinity that expressed with southern African wildlife, and takes into account the ideal tortoise habitats which (not so long ago) existed in the Maghreb (and still exist today in many places), the alleged paucity of n. African tortoise genera and species is all the more remarkable.

One answer could be that these n. African populations have never been systematically studied by experienced specialist taxonomists in modern times. Their range of diversity has been overlooked and ignored. Grotesque mistakes have been made such as classifying all small tortoises without exception as 'juveniles', and all large specimens as 'old' or, in the last century, as species which do not actually occur in the region e.g. writing of '*Testudo graeca*', actually *F. whitei*, Boulenger writing in 1891 commented;

"Old specimens have been taken for the allied *T. marginata* Shoenff, s. (syn) *campanulata* STRAUCH (by Gervais and Lallemand), the habit of which appears to be restricted to Greece".

Conclusions

The hypothesis that there is only *Testudo graeca graeca* L. 1758 in n. Africa, and that *Testudo ibera* PALLAS 1814 and *Testudo zarudnyi* NIKOLSKI 1898 are sub-species which are closely related to it is quite simply, on this evidence, no longer tenable. By direct implication, any conservation proposals based upon such a hypothesis are now revealed as hopelessly inadequate. The conservation situation is far worse than anyone has previously suspected, with many unique forms of limited distribution present rather than one widespread homogenous form; the problem of preservation is acute such are the threats facing all land tortoises in this present age.

The damage done to n. Africa's tortoise fauna by the commercial pet trade was already acknowledged as extremely serious; this new evidence of a multiplicity of species groups amplifies the probable effects of that trade to nothing less than catastrophic. One widely distributed species obviously has a much better biomass recovery potential than numerous isolated individual species of limited zoogeographic distribution.

There are, to summarise, several possible answers to the problem of why such a diverse and rich tortoise fauna (as indicated by the specimens described here) should exist in the region and where *Furculachelys* arose;

- They may represent isolated relict groups derived from the once extensive, but now extinct, chelonian fauna of what is now barren desert but was once semi-tropical forest which covered the region.
- They may have arisen by invasion from some other direction, e.g. Europe or from Asia via the Middle East, but this would require an incredible feat of convergent evolution to produce the suprapygal patterns discovered which so closely parallel those of several extant s. African forms (*Geochelone* and

Homopus) and which are unknown in extant European stock.

- The geographically central zone of distribution (eastern Algeria and Tunisia) may represent the principal relict populations of *Furculachelys*, the peripheral area of distribution (Libya, western Algeria and Morocco) being occupied partly via influxes of *Testudo* from a) the Middle East and b) via Spain. A secondary presence of *Furculachelys* may occur in Morocco via a trans-Mauritanian influx.
- If this is so, then although *Testudo* should continue to be regarded as a palaearctic form, *Furculachelys* would more accurately be regarded as a relict Ethiopian endemic originated form.

Summary of n. African distribution at generic rank

Tunisia

Analysis of osteological material indicates that *Furculachelys* is the dominant (and possibly only) genus within Tunisia. Some *Testudo* spp. may occur in the extreme south, adjacent with Libya however. There appears to be at least two species of tortoise in Tunisia, the small coastal form (*F. nabeulensis*) and a much larger inland form, as yet but little known. Material from adjacent locations in Algeria suggests that this too is likely to be a *Furculachelys* spp.

Algeria

The most striking tortoises of this region are the impressive *F. whitei*, however, Algeria also accommodates the *Terra Typica* (Oran) of *Testudo graeca*. The distribution of *Testudo* appears, on present evidence, limited to the north western zone bordering Morocco. From Algiers to the Tunisian border, the dominant forms appear to be not *Testudo* but *Furculachelys* spp.

Morocco

Testudo appears to be the dominant form at generic rank in Morocco. *Testudo graeca graeca* occurs from the Algerian border to Tangiers and throughout the Rif mountains. However, in the more westerly parts of Morocco other forms begin to appear. These have as yet been little studied and virtually no systematic data is available for them. Externally, they differ in both size and markings from *T. g. graeca* and internally feature a tripartite suprapygial (two transverse sutures). I have also examined a small number of tortoises believed to originate in the extreme western sector of Morocco which appear to conform to *Furculachelys* - however, I have not sufficient material available to permit an adequate series examination and the localities are not adequately substantiated. If confirmed however, they could represent the relicts of a trans-Mauritanian influx. It is also possible that some *Furculachelys* spp. occur inland on the eastern border with Algeria - but again, at present this must remain speculation.

Libya

The geographical position occupied by Libya is of particular relevance to the zoogeography of north African tortoise evolution. The eastern border region with Egypt (and Cyrenaica generally) accommodates a sizable population of *Testudo kleinmanni*. Further westwards, *Testudo flavominimalis* occurs. A number of other specimens examined by me from

Libya demonstrate affiliation at generic level to *Testudo*, yet fail to conform to any currently recognised species. Unfortunately, only a few isolated specimens are available, and serial study is therefore rendered impossible. I hesitate to reach any firm conclusions on the basis of such sparse evidence; yet I remain convinced that in Libya there are *Testudo* species yet to be discovered. Some very curious Libyan tortoises from the Kouf park region (also referred to under the synonym *Testudo graeca terrestris*, although very different from Wermuth's example) were described and illustrated by Schleich (1989). These animals are not at all like *T. graeca graeca* but no adequate descriptions have yet been made. The relationships of these various tortoises to each other, and to extra-territorial forms of *Testudo* and *Furculachelys* is a subject worthy of serious investigation.

This is generally suggestive of a double colonisation of *Testudo* into n. Africa via both Spain and possibly Egypt, but into an area already occupied by tortoises of southern African descent. These tortoises, represented by *Furculachelys*, remain relatively homogenous and intact at the geographical centre (Algeria-Tunisia) furthest removed from the contact points of *Testudo* in both Morocco and Libya. At the extremities of their individual ranges however, or at the interception points with *Testudo*, it is not impossible that various other forms may be found; such contacts typically giving rise to enhanced genetic diversity.

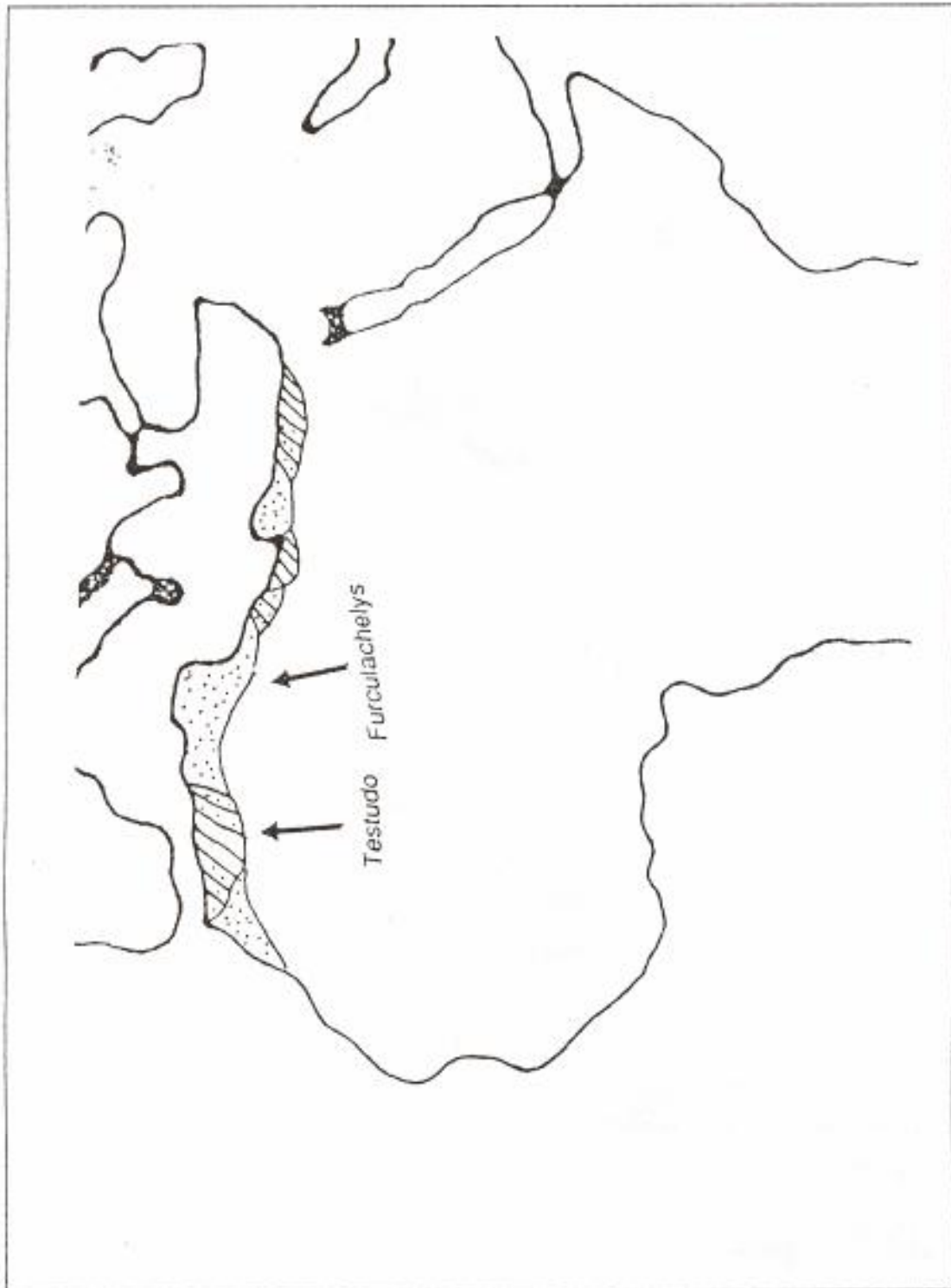
Zones of interface

The two primary interface zones, between endemic African and colonising *Testudo* forms are to be found in Libya and Morocco. Here, divergence should be most profound with a profusion of local specialisations and derived characters. Early evidence confirms this hypothesis - in both Libya and Morocco there is far less standardisation of structure than in either Algeria or Tunisia which are further removed from the primary zones of interface.

Finally, this paper raises a number of important and basic questions relating to chelonian taxonomy and distribution. In particular, the value and significance of certain basic diagnostic characters is definitely open to some doubt. In addition, the evolutionary zoogeography of Ethiopian and Holarctic tortoises requires a thorough re-examination. I by no means claim to know the answers to these many problems. Many of my hypothetical suggestions may prove not to be the case, but nonetheless demonstrate that there is a great deal we do not understand generally about these remarkable creatures. Personally, my feeling is that we know a lot less than we like to think we do.

Acknowledgements

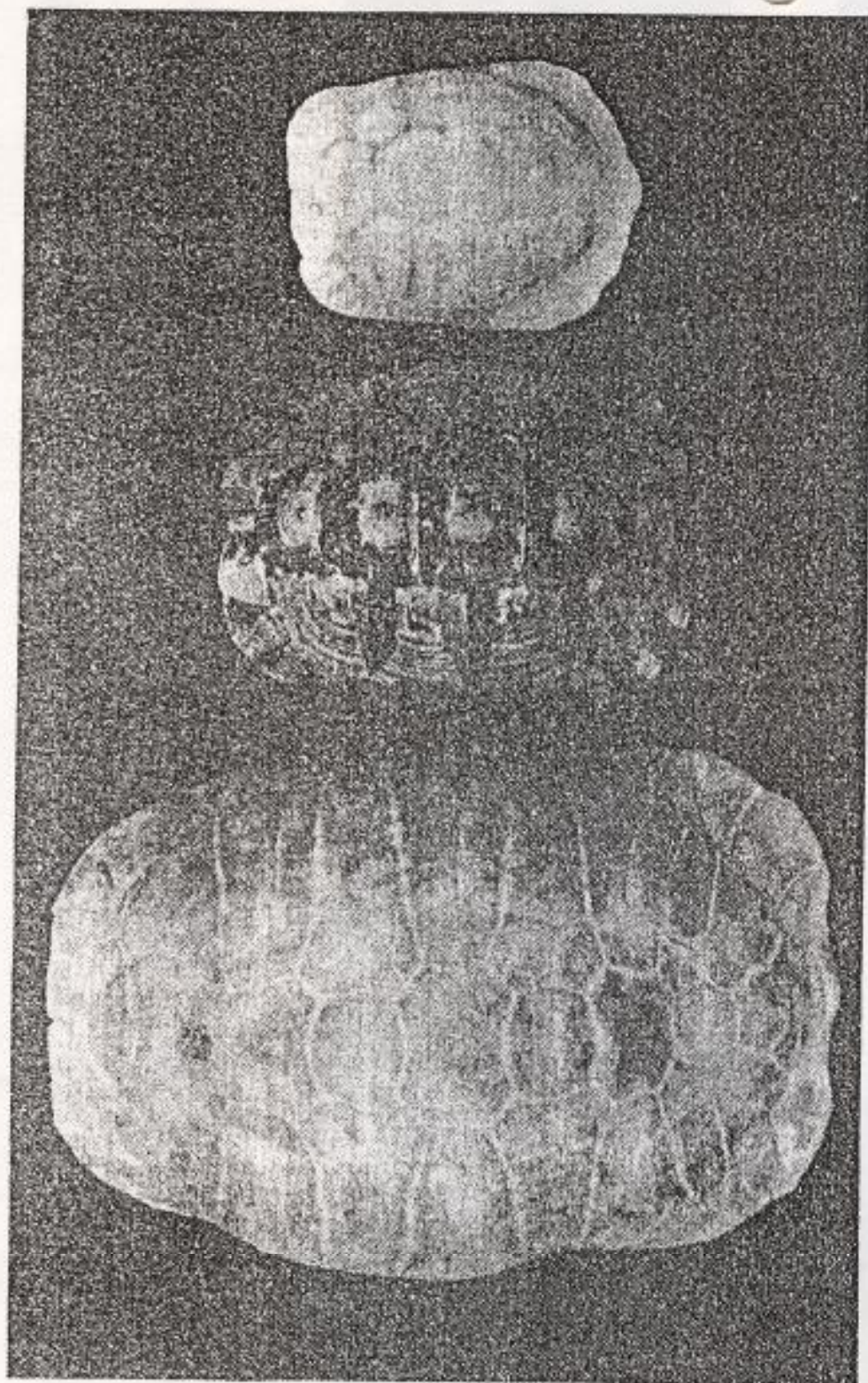
I would like to thank the following people for their assistance during this work; Jill Martin; Lin King; John Dickson (Bristol Zoo); Ms M. Hill and Ms H. Brooks; Dr. M. R. K. Lambert; I.M.S Ltd and Ms. J. Harrison for equipment sponsorship; Mrs. J. Scott; special thanks are due to the staff of the reptile section and libraries of the Natural History Museum, London.



Recorded distribution of *Testudo* and *Furculachelys* character states



Above, Holotype *F. nabeulense*



Carapace osteology: *F. whitei*, *T. g. graeca*, *F. nabeulensis* (L to R)

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