

Tortoise phylogeny and the 'Geochelone' problem

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Abstract: The taxonomy of the land tortoise family Testudinidae is revised in light of a cladistic analysis of cranial osteology. This revision agrees with recent studies in viewing the genus *Geochelone* as non-monophyletic. *Geochelone* is here restricted to two species (*G. elegans* and *G. platynota*) with other subgenera formerly assigned to 'Geochelone' raised to generic rank. The following Recent testudinid genera are recognised: *Astrochelys*; *Centrochelys*; *Chelonoidis*; *Chersina*; *Cylindraspis*; *Dipsochelys*; *Geochelone*; *Gopherus*; *Homopus*; *Indotestudo*; *Kinixys*; *Malacochersus*; *Manouria*; *Psammobates*; *Pyxis*; *Stigmochelys* and *Testudo*. The taxonomy proposed is derived from a phylogeny which is in accordance with the fossil record and a biogeographical pattern of divergence through dispersal.

Key words: *Astrochelys*, *Centrochelys*, *Chelonoidis*, *Cylindraspis*, *Dipsochelys*, *Indotestudo*, *Manouria*, phylogeny, *Stigmochelys*, Testudinidae

Introduction

The history of tortoise classification is characterised by its reliance on horizontal taxa. Originally the generic name *Testudo* was used for all terrestrial chelonians (Linnaeus 1758). A number of other, usually monospecific, genera were created in the 1800s (Bell 1828; Fitzinger 1835) and several subgenera were defined within *Testudo* (Bell 1827; Dumeril & Bibron 1835; Gray 1831; Fitzinger 1835), latter briefly raised to generic status (Gray 1869 & 1873) but subsequently disregarded. Since the middle of the 20th century a relatively consistent taxonomy has emerged in which several distinct genera of small tortoise are recognised and all comparatively large species referred to *Geochelone* (Loveridge & Williams 1957; Wermuth & Mertens 1961). This concept of *Geochelone* comprises nine Recent subgenera: *Geochelone* Fitzinger, 1835; *Chelonoidis* Fitzinger, 1835; *Cylindraspis* Fitzinger, 1835; *Manouria* Gray, 1852; *Centrochelys* Gray, 1873; *Stigmochelys* Gray, 1873; *Astrochelys* Gray, 1873 (= *Asterochelys* Gray, 1874), *Indotestudo* Lindholm, 1929 and *Dipsochelys* Bour, 1982 (= *Aldabrachelys* Loveridge & Williams, 1957; see Appendix II). The islands of the western Indian Ocean support 40% of the described supraspecific taxa and are of significance in understanding tortoise biogeography.

In recent years there has been a general move away from the broad concept of 'Geochelone', towards a usage, if not a full recognition, of the subgenera at full generic level (Bour, 1982). Partial revisions of 'Geochelone' (Crumly 1982; Gaffney & Meylan 1988) have produced various conflicting restrictions of the genus and are not widely used, with the exception of the frequent raising of *Manouria* and *Indotestudo* to generic rank (Bour 1980; Crumly 1985; Hoogmoed & Crumly 1984;

Ernst & Barbour 1989; Ernst *et al.* 2000; Meylan & Sterrer 2000).

This study aims to provide a morphological phylogeny of the taxa historically placed in ‘*Geochelone*’ on which to base a more objective revision of the genus. Previous studies have examined relatively few characters (Crumly 1982; Gaffney & Meylan 1988; Meylan & Sterrer 2000). A review of previous taxonomic systems was combined with a study of skeletal material. This allowed existing systems to be compared to the results of analyses based on cranial osteological characters.

Material & methods

Cranial osteological material of all recent tortoise genera/subgenera was examined (Table 1; Figs. 1-4) and the state of a set of characters recorded. In order to eliminate individually or ontogenetically variable characters, as many specimens of each taxon were examined as was practical. In each case all definable characters were recorded; once all the specimens had been examined variable characters and single species autapomorphies were excluded from further analysis. All characters used in previous osteology based classifications and phylogenetic studies (Gray 1873; Loveridge & Williams 1957; Gaffney 1979;

Table 1. Material examined (nomenclature modified from Ernst *et al.*, 2000)

Taxon	Number examined	Location
<i>Acynonyx planicauda</i>	3	MNHN, private collections
<i>Batagur baska</i>	5	OUM, private collections
<i>Chersina angulata</i>	2	BM(NH), private collections
<i>Geochelone (Astrochelys) radiata</i>	13	MNHN, BM(NH)
<i>G. (A.) yniphora</i>	1	MNHN
<i>G. (Centrochelys) sulcata</i>	5	BM(NH), private collections
<i>G. (Chelonoidis) carbonaria</i>	15	UMZ, OUM, BM(NH), private collections
<i>G. (Cylindraspis) bourbonica</i>	20	MNHN
<i>G. (Dipsochelys) dussumieri</i>	28	BM(NH), UMZ, MNHN, NPTS, OUM, private collections
<i>G. (G.) elegans</i>	9	private collections
<i>G. (Stigmochelys) pardalis</i>	2	BM(NH), UMZ
<i>Gopherus polyphemus</i>	5	BM(NH), private collections
<i>G. (Xerobates) agassizii</i>	4	BM(NH), private collections
<i>Heosemys grandis</i>	5	BM(NH), private collections
<i>Homopus areolatus</i>	4	MNHN, private collections
<i>Indotestudo elongata</i>	3	BM(NH), private collections
<i>Kinixys erosa</i>	2	BM(NH), private collections
<i>Malacochersus tornieri</i>	5	BM(NH), private collections
<i>Manouria emys</i>	4	BM(NH), UMZ, private collections
<i>Psammobates geometricus</i>	3	UMZ, private collections
<i>Pyxis arachnoides</i>	2	BM(NH), private collections
<i>Testudo graeca</i>	15	OUM
<i>T. (Agrionemys) horsfieldi</i>	6	UMZ, private collections
<i>T. (Pseudotestudo) kleinmanni</i>	2	private collections

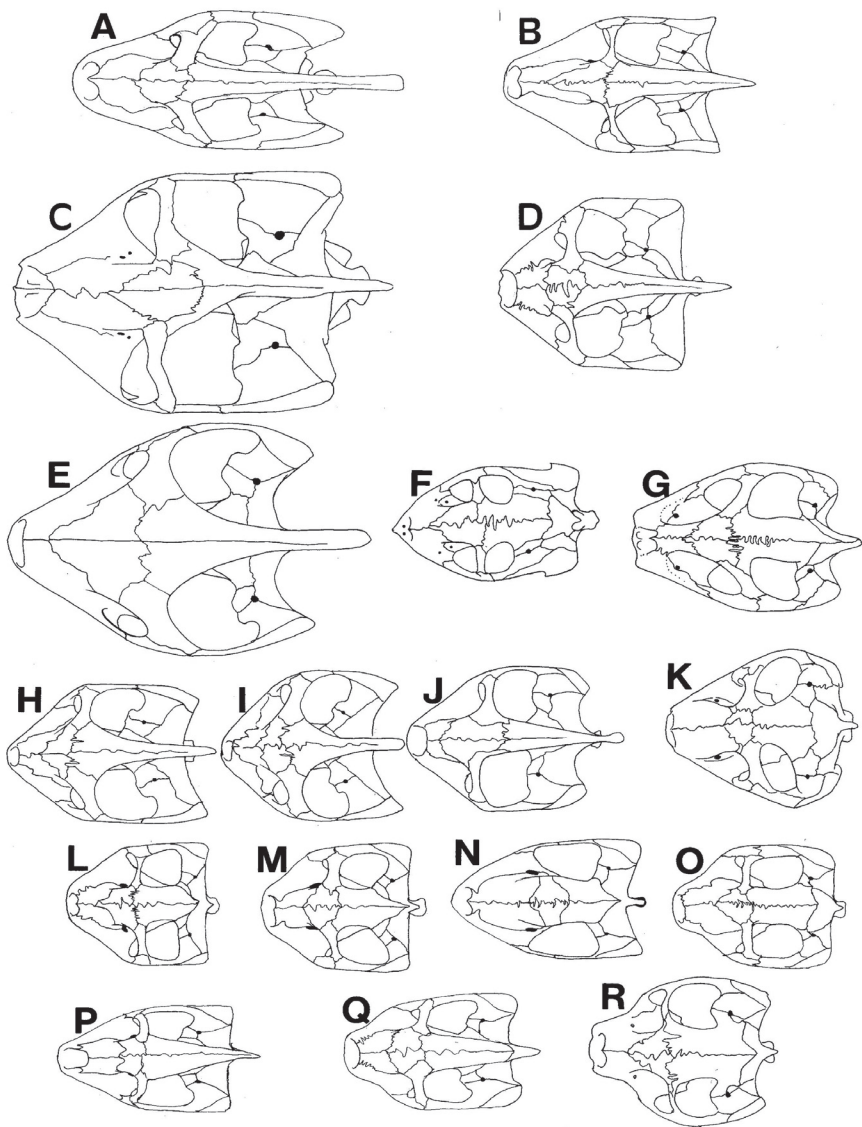


Fig. 1. Tortoise skulls in dorsal view

a). *Manouria emys*, b). *Centrochelys sulcata*, c). *Dipsochelys dussumieri*, d). *Stigmochelys pardalis*, e). *Cylindraspis bourbonica*, f). *Pyxis arachnoides*, g). *Geochelone elegans*, h). *Astrochelys radiata*, i). *'Astrochelys' yniphora*, j). *Chelonoidis carbonaria*, k). *Gopherus polyphemus*, l). *Psammobates geometricus*, m). *Homopus areolatus*, n). *Kinixys erosa*, o). *Malacochersus tornieri*, p). *Chersine angluata*, q) *Indotestudo eleongata*, r) *Testudo graeca*

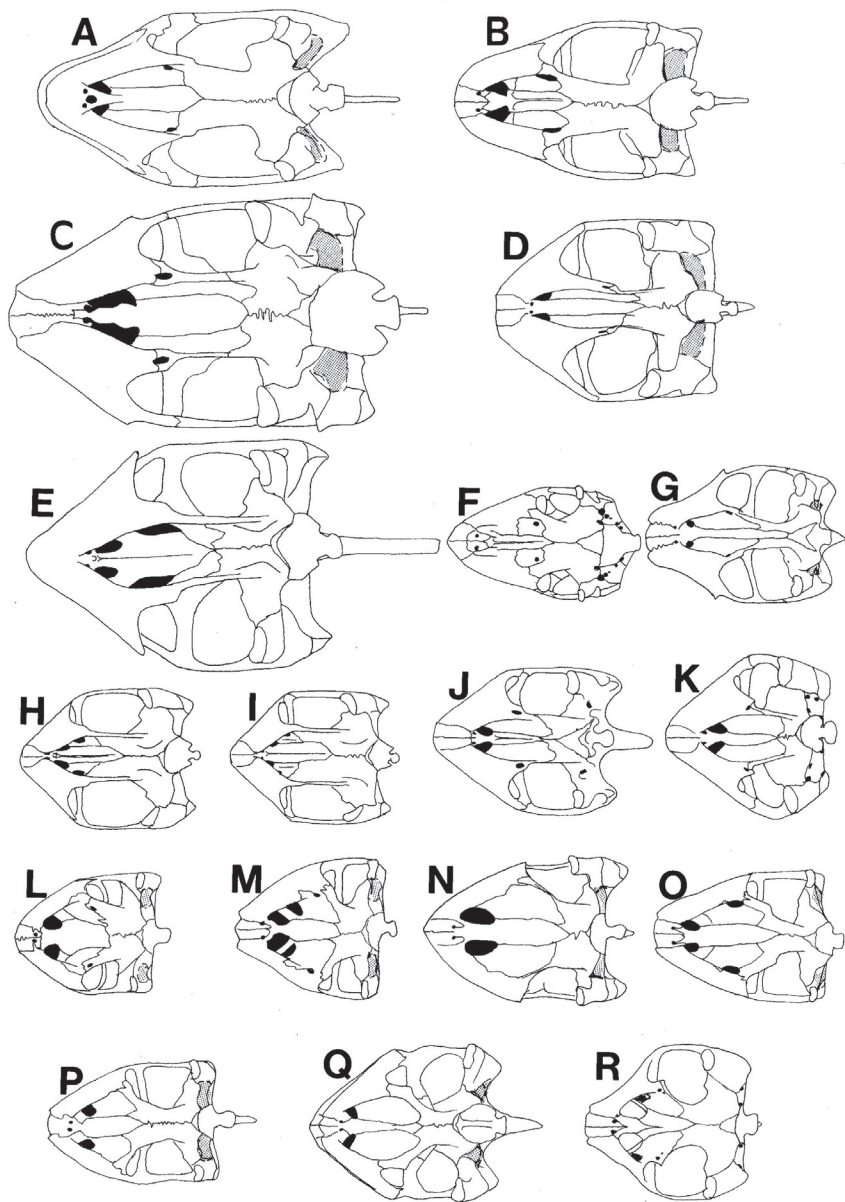


Fig. 2. Tortoise skulls in ventral view. Fenestra postotica stippled.

a). *Manouria emys*, b). *Centrochelys sulcata*, c). *Dipsochelys dussumieri*, d). *Stigmochelys pardalis*, e). *Cylindraspis bourbonica*, f). *Pyxis arachnoides*, g). *Geochelone elegans*, h). *Astrochelys radiata*, i). '*Astrochelys*' *yniphora*, j). *Chelonoidis carbonaria*, k). *Gopherus polyphemus*, l). *Psammobates geometricus*, m). *Homopus areolatus*, n). *Kinixys erosa*, o). *Malacochersus tornieri*, p). *Chersine angluata*, q) *Indotestudo eleongata*, r) *Testudo graeca*

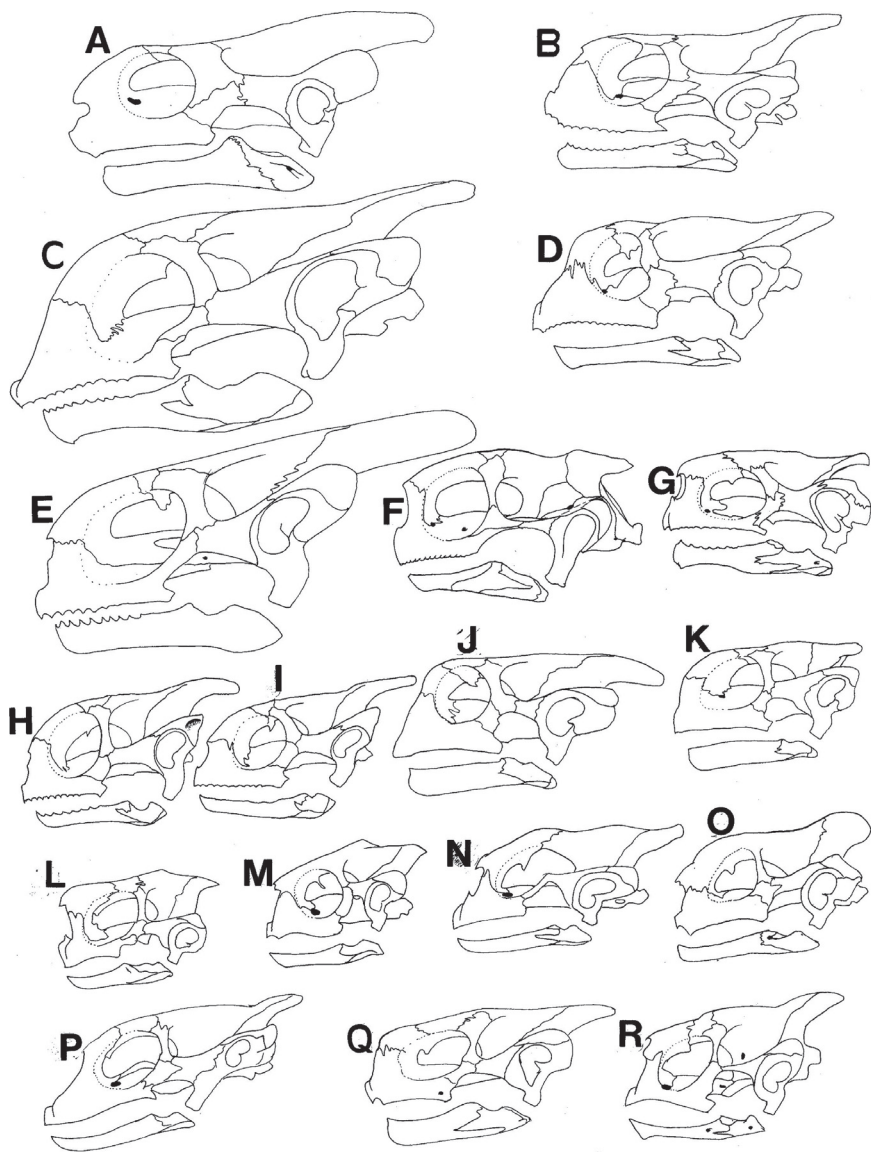


Fig. 3. Tortoise skulls in lateral view

a). *Manouria emys*, b). *Centrochelys sulcata*, c). *Dipsochelys dussumieri*, d). *Stigmochelys pardalis*, e). *Cylindraspis bourbonica*, f). *Pyxis arachnoides*, g). *Geochelone elegans*, h). *Astrochelys radiata*, i). *'Astrochelys' yniphora*, j). *Chelonoidis carbonaria*, k). *Gopherus polyphemus*, l). *Psammobates geometricus*, m). *Homopus areolatus*, n). *Kinixys erosa*, o). *Malacochersus tornieri*, p). *Chersine angluata*, q) *Indotestudo eleongata*, r) *Testudo graeca*

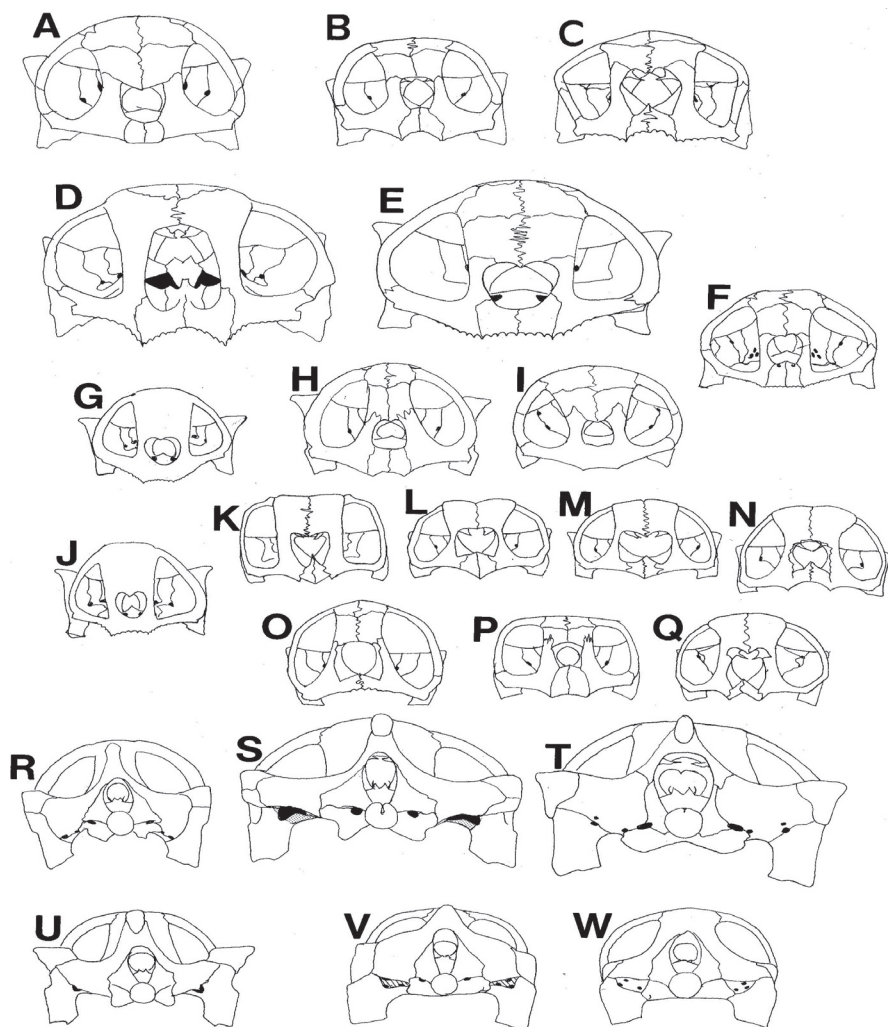


Fig. 4. Tortoise skulls in anterior and posterior views. a-q) anterior view. r-w) posterior view, showing condition of postotic fenestra.

a). *Manouria emys*, b). *Centrochelys sulcata*, c). *Stigmochelys pardalis*, d). *Dipsochelys dussumieri*, e). *Cylindraspis bourbonica*, f). *Pyxis arachnoides*, g). *Astrochelys radiata*, h). *Chelonoidis carbonaria*, i). *Gopherus polyphemus*, j). *'Astrochelys' yni-phora*, k). *Psammobates geometricus*, l). *Homopus areolatus*, m). *Kinixys erosa*, n). *Malacochersus tornieri*, o). *Chersine anguata*, p). *Indotestudo eleongata*, q). *Testudo graeca*, r). *Stigmochelys pardalis* (partially closed by descending opisthotic), s). *Dipsochelys dussumieri* (fenestra open - stippled area), t). *Cylindraspis bourbonica* (closed by opisthotic contacting exoccipitals), u). *Chelonoidis carbonaria*, (closed by opisthotic contacting the pterygoids), v). *Gopherus polyphemus* (closed by ossification), w). *Testudo graeca* (closed by partial ossification)

Bour 1982, 1984 & 1994; Bramble 1982; Crumly 1982; Gerlach & Canning 1998; Meylan & Sterrer 2000) were examined. The characters selected for use in phylogenetic analysis are described below. Terminology is derived from Gaffney (1979).

Abbreviations

Institutional abbreviations are as follows:

BM(NH) = British Museum (Natural History)

UMZ = University Museum of Zoology, Cambridge

MNHN = Museum nationale d'Histoire naturelle, Paris

NPTS = Nature Protection Trust of Seychelles

OUM = Oxford University Museum

Outgroup selection

The Testudinidae and Bataguridae are believed to share a close phylogenetic relationship. They may be sister taxa (Gaffney 1979) or the batagurids may be paraphyletic with regard to testudinids (Hirayama 1984; Gaffney & Meylan 1988). Two batagurid species were therefore used as outgroups: *Batagur baska* and *Heosemys grandis*.

Characters examined

1. Frontal excluded from the orbit.
2. Processus circumolfactorius large, reducing the width of the fossa nasalis by at least half.
3. Sulcus olfactorius closed ventrally at level of processus circumolfactoris
4. Median suture of frontals more than twice as long as that between the prefrontals.
5. Angle of postorbitals at junction with skull roof - coded as $<15^\circ=0$, $>15^\circ=1$
6. Low temporal arch - defined as the top of the suture between the postorbital and quadratojugal lying below the highest point of the quadrate.
7. Degree of temporal emargination - the narrowness of the temporal arch has been used in previous studies, generally subjectively. Here a measure of the contact between parietal and postorbital is used. Broad contact (parietal-postorbital suture length equal to parietal-frontal) = 0. Reduced (parietal-frontal suture 1.5 times as long as parietal-postorbital) = 1. Narrow (parietal-frontal suture 3 times as long as parietal-postorbital) = 2.
8. Lingual edge of premaxilla lacking ventral ridge - this is caused by the maxillary alveolar ridges contacting behind the premaxillae and obscuring the foramina praepalatina.
9. Labial border of premaxilla tricuspid - the jaws may be bicuspid or tricuspid, this is most apparent on the horny beak but is reflected by the underlying bone. Coded as bicuspid = 0, tricuspid = 1.
10. Shallow premaxillae - premaxillary symphysis depth shallower than height of narial opening = 0, symphysis shallower than narial opening, with dorsal projection = 1, symphysis depth exceeds height of narial opening = 2.

11. Longitudinal ventral ridge along premaxillary symphysis.
12. Longitudinal ventral ridge along maxilla-premaxilla suture.
13. Lingual ridge on maxilla = 0, or extending onto premaxillae = 1.
14. Lingual surface of labial ridge of premaxilla with tooth-like tubercles.
15. Lingual surface of labial ridge of maxilla with tooth-like tubercles.
16. Labial ridge of maxilla strongly toothed (tubercle height at least equal to diameter).
17. Tooth-like tubercles on maxillary alveolar ridges.
18. Maxillae curved in lateral view.
19. Maxillae not projecting posteriorly beyond postorbitals.
20. Pit in anterior part of maxillary alveolar ridge.
21. Vomer wide between foramina praepalatina - defined as the vomer width being approximately equal to the combined width of the premaxillae.
22. No ventral ridge on vomer
23. Dorsal crest at mid point of parietal suture not raised above supraoccipital.
24. Vomer elongated posteriorly, dividing pterygoids as well as palatines
25. Foramen orbito-nasale visible ventrally.
26. Foramen orbito-nasale large.
27. Foramina praepalatina small.
28. Foramina praepalatina not visible in ventral view - foramina may be concealed by lingual extensions of the maxillary alveolar ridges.
29. Palatine extends onto triturating surface of upper jaw.
30. Longitudinal ventral ridges on palatines.
31. Vomer and palatines not arched dorsally.
32. Inflated tympanic chamber - the medio-dorsal surface of the quadrate is convex, covering an enlarged ethmoid region.
33. Otolith within otic region.
34. Ridge on suture of incisura columella auris on quadrate - this is the ridge on the commisura quadrati of Bour (1984).
35. Canalis chorda tympani quadrati not enclosed.
36. Processus interfenestralis obscured in posterior view.
37. Squamosal with dorsal process - posterodorsal surface of squamosal extended above surface of antrum postoticum.
38. Antrum postoticum well developed posteriorly - this character is here defined as the extension of the squamosal covering the antrum postoticum extending behind the basioccipital condyle.
39. Dorsoventral ridge on processus inferior parietalis - a ridge running from the quadrate to the parietals is always present and highly developed in *Cylindraspis* spp. but is absent or only weakly developed in other taxa. In this study it has been defined as a ridge projecting into the fossa temporalis at least half as far as does the processus trochlearis oticum = 2, ridge present but not projecting = 1.
40. Tuberculae on posterior margin of pterygoids.
41. Pterygoids ventrally concave along basisphenoid suture.
42. Large supraoccipital crest - defined as crest projecting posteriorly beyond the

- basioccipital condyle and raised above the parietals.
43. Supraoccipital crest reinforced by horizontal keels.
 44. Overhang of supraoccipital crest continuing onto postorbital.
 45. Processus inferior parietalis contacts quadrate, prootic partly covered.
 46. Ventral depression on basisphenoid or anterior margin of basioccipital.
 47. Depression on basioccipital (in addition to depression on basisphenoid).
 48. Longitudinal ventral ridge on ventral surface of condylus basioccipitalis.
 49. Tuberculae of basioccipital projecting- here defined as projecting beyond posterior margin of opisthotic.
 50. Fenestra postotica obscured: 0 = not obscured, 1 = obscured by opisthotic contacting exoccipitals (opisthotic descending and exoccipitals dorsally extended), 2 = obscured by ossification, 3 = reduced by partial ossification from posteroventral margin of opisthotic, resulting in partial ventral contact with pterygoids. The obscuring of the fenestra by descent of the opisthotic (without raising of the exoccipitals) is autapomorphic for *Stigmochelys pardalis* and the opisthotic descending to the pterygoid is autapomorphic for *Chelonoidis* spp. and these states were not included in analysis
 51. Foramen externum nervi glossopharyngei separated from fenestra postotica.
 52. Foramen chorda tympani inferius clearly separated from fenestra postotica
 53. Foramen posterius canalis carotici interni well separated from quadrate - in most chelonians the foramen canalis carotici passes through the pterygoid-quadrate suture (0), in some testudinids it is entirely enclosed by the pterygoid (1).
 54. Processus trochlearis oticum projects anteriorly - here defined as the length of the projection being at least equal to half the width.
 55. Os transiliens present.
 56. Single foramen nervi trigemini - the foramen may be split into two by the descending processus inferior parietalis. This has also been referred to as the sphenoidal foramen (Bour 1984), it is a variable character in most species. In this study the foramen is considered single if only one opening is visible or if two foramina are close together (distance between the foramina being less than the diameter of the larger foramen).
 57. Palatine circulation more developed than stapedal - shown by the foramen caroticum laterale being larger than the foramen stapedo-temporale.
 58. Arteria mandibularis passing through the foramen cavernosum - presence of the foramen arterio-mandibulare within the incisura prootica of Bour (1984).
 59. Arteria mandibularis separated from foramina nervi trigemini by prootic and pterygoid.
 60. Anterior reduction of lingual dentary ridge - a slight ridge (<1mm) may be retained (1) or the ridge may be completely absent (0).
 61. Horizontal ventral ridge either side of dentary symphysis.
 62. Anterior process of surangular interdigitates with dentary in adult.

Node Characterisation

1. Testudinidae

All land tortoises are united on the basis of loss of the longitudinal ridges on the palatines (30), Bootstrap value = 100.

2. *Manouria* (*M. emys*, *M. impressa*)

The plesiomorphic extension of the palatine onto the triturating surface of upper jaw (30) in *Manouria* may be associated with their partially aquatic feeding habits, at least in *M. emys* (Wirot, 1979), as in the batagurines. The retention of the horizontal ventral ridge either side of symphysis (61) may be associated with the retention of the class II mental glands found in the batangurines (Winokur & Legler 1975).

3. Testudinidae excluding *Manouria*

The main group of tortoises share the exclusion of the palatines from the triturating surface of the upper jaw (29), the loss of the horizontal ridge on either side of the dentary symphysis (61) and the arteria mandibularis being separated from the foramina nervi trigemini (62). Post-cranial autapomorphies include the development of quadrilateral and octagonal neurals (reversed to the plesiomorphic hexagonal shape in *Malacochersus*, *Psammobates* + *Homopus* and *Chersina* + *Kinyxis*). This corresponds to node 2 in Gaffney & Meylan (1988). Bootstrap value = 98.

4. large African tortoises + western Indian Ocean tortoises

This group contains most of the large tortoises usually included in '*Geochelone*', however, it does not include *Geochelone* (sensu stricto). Defined by the premaxilla extending posteriorly to contact the palatines (2) and the processus circumolfactorius being large, reducing the width of the fossa nasalis by at least half (4). Bootstrap value = 100.

5. *Centrochelys sulcata*

This monotypic genus is defined by the anteriorly enlarged vomer, forming a ventral shelf at contact with premaxillae and the processus pterygoideus externus projecting distinctly.

6. *Stigmochelys* + western Indian Ocean region tortoises

Defined by the sulcus olfactorius being closed ventrally at the level of the processus circumolfactorius (5) and the tooth-like tubercles on the lingual surface of the labial maxillary ridge (15). Post-cranial autapomorphies include the development of relatively large inguinal scutes. Bootstrap value = 100.

7. *Stigmochelys* + *Dipsochelys*

Members of this clade are united by the frontal being excluded from the orbit (1). Bootstrap value = 96.

8. *Stigmochelys pardalis*

This monotypic genus is defined by the anteriorly curved maxillary lingual ridge

and the foramen postotica being obscured by the descent of the opisthotic.

9. *Dipsochelys* (*D. arnoldi*, *D. dussumieri*, *D. grandidieri*, *D. hololissa*, *D. abrupta*)

The Seychelles-Maladagascar giants are a well defined group. Autapomorphies are: narial opening higher than wide, prefrontal contacting postorbitals and posterior elongation of the premaxilla. The narial opening modification and the presence of the processus dorsalis vomerinus are characters associated with the ability of these tortoises to drink through their nasal passages (Arnold 1979; Bour 1982; Gerlach & Canning 1998).

10. *Pyxis* + *Astrochelys* + *Cylindraspis*

These taxa are united by the obscuring of the fenestra postotica by the opisthotic contacting the exoccipitals (50). Bootstrap value = 96.

11. *Astrochelys* + *Cylindraspis*

Defined by the longitudinal ventral ridge along the maxilla-premaxilla suture (14) and the horizontal keels on the supraoccipital crest (41). Bootstrap value = 100.

12. *Astrochelys radiata* + *Cylindraspis*

These taxa are united by the possession of a well developed ridge on the processus inferior parietalis (39), associated with the jaw musculature (Gerlach 1999). Bootstrap value = 100. (*A. radiata* Fig 1h, 2h, 3h, 4g)

13. *Cylindraspis* (*C. bourbonica*, *C. inepta*, *C. peltastes*, *C. triserrata*, *C. vosmaeri*)

There are no cranial autapomorphies for this group, which is effectively a monophyletic group of giant *Astrochelys* tortoises and could be considered to be a subgenus of *Astrochelys*. (Fig. 1e, 2e, 3e, 4e&t)

14. *Pyxis* (*P. arachnoides* + *P. (Acinyxis) planicauda*)

The monotypic Malagasy 'genera' *Pyxis* and *Acinyxis* are closely related and were originally contained within *Pyxis*, a classification which would be recommended by previous studies (Bour 1981) and is supported by this analysis. The two taxa share the open canalis chorda tympani quadrati (35), this is of unknown significance and is shared by one of the outgroups (*Batagur baska*). They also have an identical pit in the anterior part of the maxillary alveolar ridge (20). *P. arachnoides* is distinctive in possessing a plastral hinge between the epiplastra and hyoplastra underlying the humeral and pectoral scutes. Bootstrap value = 100.

15. *Geochelone* + *Malacochersus* + *Psammobates* + *Homopus* + *Chersina* + *Kinyxis* + *Chelonoids* + *Gopherus* + *Indotestudo* + *Testudo*

Defined by the narrow temporal arch (7). Post-cranial autapomorphies include suprapygals united or separated by a straight suture. Bootstrap value = 100.

16. *Geochelone* (*G. elegans*, *G. platynota*)

The only cranial autapomorphy in this genus is the antero-ventrally directed anterior prefrontal symphysis projection; post-cranially it resembles other moderately sized, domed tortoises.

17. *Malacochersus* + *Psammobates* + *Homopus* + *Kinixys* + *Chersina* + *Chelonoidis* + *Gopherus* + *Testudo* + *Indotestudo*

This corresponds to a restricted Testudininae (Gaffney & Meylan 1988) excluding most *Geochelone* (sensu lato). The Testudininae was originally named by Siebenrock (1909) and defined by Loveridge & Williams (1957) on the basis of a set of variable or symplesiomorphic characters. Defined by the lack of tooth-like tubercles on the lingual surface of premaxilla labial ridge (16); post-cranial autapomorphies include the development of a nuchal. Bootstrap value = 94.

18. Neotropical and Nearctic tortoises (*Gopherus* + *Chelonoidis*)

Defined by the deep premaxillary symphysis (10). Bootstrap value = 100.

19. *Gopherus* (*G. agassizii*, *G. berlandieri*, *G. flavomarginata*, *G. polyphemus*)

Gopherus is defined by the sulcus olfactorius closed ventrally at level of processus circumolfactoris (3), lingual edge of premaxilla lacking ventral ridge (8), longitudinal ventral ridge along premaxillary symphysis (11), lingual maxillary ridge extending onto premaxillae (13), vomer and palatines not arched dorsally (31), inflated tympanic chamber (32), otolith within otic region (33), fenestra postotica obscured by ossification (50), os transiliens present (55). Of cranial characters the extreme inflation of the tympanic chamber, the very large otolith and the possession of an enlarged stapedal footplate have been described as characters uniting *G. polyphemus* and *G. flavomarginatus* in the subgenus *Gopherus sunsu stricto* with *G. agassizi* and *G. berlandieri* in the subgenus *Xerobates* (as '*Scaptochelys*'; Bramble 1982). Of these characters the enlarged stapedal footplate has not been widely examined although Bramble (1982) stated that the *G. agassizi* ratio of stapes length to footplate diameter of 28:1 is similar to that of other testudinids in contrast to the ratio of 3-8:1 in *Gopherus s. s.* of (Bramble 1982). A low ratio is also found in *Dipsochelys hololissa* (6:1) and may be more widespread. The monophyly of *Gopherus* is supported by their possession of class I mental glands (Winokur & Legler 1975). Bootstrap value = 100.

Gaffney & Meylan's Xerobatinia (1988) comprises *Gopherus* and very similar fossil genus *Stylemys* which share the longitudinal ventral ridge on the premaxillary symphysis (14).

20. *Chelonoidids* (*C. carbonaria*, *C. chilensis*, *C. denticulata*, *C. nigra*)

The South American tortoises are united by the anterior reduction of the lingual dentary ridge to a low ridge and the obscuring of the fenestra postotica by the opisthotic contacting the pterygoids and the presence of a ridge running from the postero-dorsal margin of the cavum tympani to the dorsal squamosal projection.

21. *Indotestudo* + *Malacochersus* + *Psammobates* + *Homopus* + *Kinyxis* + *Chersina* + *Testudo*

These species are not united by any cranial autapomorphies. Bootstrap value = 100.

22. *Indotestudo* (*I. elongata*, *I. forsteni*)

This genus is defined by the ventral ridge on the basioccipital extending onto the basisphenoid; post-cranial autapomorphies include the humero-pectoral suture crossing the entoplastron.

23. Small African and European tortoises (*Malacochersus* + *Psammobates* + *Homopus* + *Kinyxis* + *Chersina* + *Testudo*)

These species are united by the curvature of the dentary symphysis (64). Bootstrap value = 98.

24. *Chersina* + *Kinyxis*

These genera are united by the lack of a ventral ridge on the vomer (22) and the presence of tuberculae on the pterygoids (40). The neural bones have reverted to the plesiomorphic hexagonal shape. Bootstrap value = 100.

25. *Chersina angulata*

This monotypic genus has a distinctively elongated skull, with a sloping nasal region.

26. *Kinyxis* (*K. belliana*, *K. erosa*, *K. homeana*, *K. natalensis*)

This genus is defined by the symphysial separation of the dentary grooves. The carapace is highly distinctive with the possession of infra-marginal scutes and a hinge in the carapace between the 4th and 5th costals and 7th and 8th peripherals.

27. *Homopus* + *Psammobates* + *Malacochersus* + *Testudo*

These tortoises are not united by any autapomorphies, although they are all notable in having short, high skulls (although proportions of height and length overlap with those of *Gopherus* spp.) . Bootstrap value = 100.

28. *Psammobates* + *Homopus*

These genera are united by the raised crest on the midpoint of the parietal suture (23). Post-cranial autapomorphies include the possession of a protuberant 'hip spine' (Gaffney & Meylan 1988). Bootstrap value = 100.

29. *Psammobates* (*P. geometricus*, *P. oculifera*, *P. tentorius*)

This genus is defined by the supraoccipital crest forming a short, descending spine.

30. *Homopus* (*H. areolatus*, *H. boulengeri*, *H. femoralis*, *H. signatus*)

This genus is not defined by any cranial autapomorphies.

31. *Malacochersus* + *Testudo*

These genera are united by the processus inferior parietalis contacting the quadrate and partly covering the prootic (45). Bootstrap value = 100.

32. *Malacochersus tornieri*

This monotypic African genus is defined by the short rounded supraoccipital crest. It is distinctive genus with a flattened shell and reduced ossification.

33. *Testudo* (*T. graeca*, *T. hermanni*, *T. horsfieldii*, *T. kleinmanii*)

This genus is defined by the reduction of the fenestra postotica by partial ossification (50). Of the *Testudo* species *T. horsfieldii* is the most plesiomorphic, lacking the plastral hinge between the femoral and abdominal scutes and can be considered a distinct subgenus (*Agrionemys*). Cranial osteology does not support the recognition of *Pseudotestudo* as a distinct subgenus. Bootstrap value = 96.

Taxonomy

Geochelone (sensu lato) was recognised by Loveridge & Williams (1957) based on plesiomorphies (skull “remarkably primitive, surprisingly uniform; tendency for down-growth of opisthotic to conceal fenestra postotica in posterior view”). These authors defined the genus as possessing external nares not higher than wide; quadrate enclosing stapes; postotic fenestra not concealed in posterior view; nuchal absent; anterior neurals alternately octagonal and quadrilateral; first dorsal vertebrae short and stout; supracaudal undivided, gulars paired but not divergent; entoplastron not crossed by humeropectoral sulcus (Loveridge & Williams 1957). Within *Geochelone* they recognised 7 subgenera: *Astrochelys* (as *Asterochelys*), *Chelonoidis*, *Cylindraspis*, *Dipsochelys* (as *Aldabrachelys* - see Appendix II), *Geochelone*, *Indotestudo* and *Manouria*. The phylogeny proposed here identifies these characters as either variable or plesiomorphic, supporting views that *Geochelone* (sensu lato) is a paraphyletic grouping (Bour 1980 & 1984; Crumly 1985; Gaffney & Meylan 1988; Ernst & Barbour 1989; Ernst *et al.* 2000; Meylan & Sterrer 2000).

If the broad usage of *Geochelone* (as in Loveridge & Williams 1957) were retained it would include all tortoises and would effectively revert to the original usage of ‘*Testudo*’. Maintaining the distinctiveness of the genera that are well defined on general morphological grounds (*Testudo*, *Malacochersus*, *Psammobates*, *Homopus*, *Chersina*, *Kinyxis*, *Pyxis* and *Gopherus*) requires the recognition of the following additional monophyletic genera: *Astrochelys*, *Centrochelys*, *Chelonoidis*, *Cylindraspis*, *Dipsochelys*, *Geochelone*, *Indotestudo*, *Manouria* and *Stigmochelys*. This arrangement agrees with recent revisions proposed by Bour (1980, 1984) but differs from earlier phylogenies. Most previous studies of testudinid relationships have produced largely unresolved phylogenies (e.g. Williams 1952; Loveridge & Williams 1957) or widely differing results.

The arrangement proposed by Williams (1952) and Loveridge & Williams (1957) defined only two suprageneric groupings. Of these the †*Stylemys* + *Gopherus* clade is accepted by most workers (e.g. Auffenberg 1966 & 1971; Crumly 1985; Gaffney & Meylan 1988) whilst the ‘*Geochelone*’ characters are symplesiomorphies

as noted above. Auffenberg (1966) supported the †*Stylemys* + *Gopherus* clade and suggested an affinity with *Testudo* on the basis of the arrangement of carpal bones. This review also suggested relationships between *Geochelone* (sensu stricto), *Centrochelys* and *Chelonoidis*. Carpal morphology provided very little resolution, largely because of the degree of fusion of carpal bones having major functional implications (Auffenberg 1966). In a subsequent reappraisal of the relationships between western hemisphere taxa Auffenberg (1971) expanded the †*Stylemys* + *Gopherus* clade to include †*Hesperotestudo* and †*Cymacolthus* and suggested a relationship between these and *Chelonoidis* (which he considered a subgenus of *Geochelone*) rather than *Testudo*. He considered these taxa to be a sister group to *Manouria*.

Subsequent arrangements (Auffenberg 1974; Crumly 1985) were combined into a phylogeny by Gaffney & Meylan (1988). This agreed with the present phylogeny in having a basal *Manouria* and in the division of *Geochelone* (sensu lato) although the precise arrangement of the diminutive African forms differs. Although each of the nodes is supported by at least one autapomorphy the data set is very restricted and includes a number of post-cranial characters that may be functionally convergent and characters of high variability (such as head squamation). Of the groupings proposed the Megalochelyini (excluding †*Megalochelys* which is too fragmentary to be reliable; Bour 1994 and *pers. obs.*), *Homopus* + *Psammobates*, *Pyxis* + *Acinixys* are supported by the present study as are the basal position of *Manouria* and the generally derived nature of the smaller taxa. If the locomotory (calcaneum and astragalus fusion, carpal fusion, large medial centrale, epicondylar foramen and intertrochanteric fossa size), variable (division of supracaudal, latissimus dorsi scar, position of foramen posterior canalis carotici, arrangement of incisura columella auris, nuchal scute shape, squamation) and uncertain functional significance (penis shape, trachaea length) are excluded the resolution is reduced with the position of the Xerobatina becoming unresolved and the relationships between the smaller testudinids being uncertain. The only stable groups are the ones proposed in the present study with the exception of the *Chelonoidis* + *Geochelone* (*Geochelone*, *Centrochelys* and *Stigmochelys*) clade. It should be noted that this pairing is united only by the lack of a nuchal scute which appears occasionally in at least some other taxa (e.g. *Dipsoschelys dussumieri*). The phylogeny proposed by Meylan & Sterrer (2000) supports the widespread recognition of the basal position of *Manouria*. This classification recognises three major groupings; a modified Xerobatinae (*Gopherus* and fossil forms), ‘*Geochelone*’ (sensu lato) and the ‘diminutive African forms’. Meylan & Sterrer (2000) define their ‘*Geochelone* in the broad sense’ on the basis of a completely enclosed entepicondylar foramen and a gular usually not in contact with the entoplastron. Neither of these characters are autapomorphies; the enclosure of the entepicondylar foramen being found in *Gopherus* and some *Manouria*, and the gular contacting the entoplastron in some ‘*Geochelone*’ but not in *Pyxis* and *Homopus*, and being variable in *Chersina* and *Kinyxis*.

Other studies have little application to phylogeny; Williams (1950) recognised distinct groups based on cervical articulation, but these do not follow any recognisable taxonomic arrangement (even below generic level). Gray’s (1873) ‘sections’ have some relation to phylogeny with section I comprising the Xero-

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batina (*Xerobates*, *Gopherus*), Megalochelyina (*Chelonoidis nigra*, *Dipsochelys*, *Astrochelys*) and Chelonoidina (*Chelonoidis* and *Manouria*); section II Peltastina (*Psammobates*, *Centrochelys*, *Testudo*, *Chersina*); section III Homopina (*Homopus*) and Pyxidina (*Pyxis*) and section IV Kinixyina (*Kinixys*). These arrangements have not been used subsequently with the exception of a reduced Megalochelyina (restricted to *Dipsochelys* and *Astrochelys*).

The phylogeny proposed here results in recognition of the following genera:

Family Testudinidae

'Astrochelys' yniphora

Astrochelys Gray, 1873 (*A. radiata*)

Centrochelys Gray, 1872 (*C. sulcata*)

Chelonoidis Fitzinger, 1835 (*C. carbonaria*, *C. chilensis*, *C. denticulata*, *C. nigra*)

Chersina Gray, 1831 (*C. angulata*)

Cylindraspis Fitzinger, 1835 (*C. bourbonica*, *C. inepta*, *C. peltastes*, *C. triserrata*, *C. vosmaeri*)

Dipsochelys Bour, 1982 (*D. arnoldi*, *D. dussumieri*, *D. grandidieri*, *D. hololissa*, *D. abrupta*)

Geochelone Fitzinger, 1835 (*G. elegans*, *G. platynota*)

Gopherus Rafinesque, 1832

Gopherus (*G. (G.) berlandieri*, *G. (G.) polyphemus*)

Xerobates Agassiz, 1857 (*G. (X.) agassizii*, *G.(X.) flavomarginata*)

Homopus Duméril & Bibron, 1835 (*H. areolatus*, *H. boulengeri*, *H. femoralis*, *H. signatus*)

Indotestudo Lindholm, 1929 (*I. elongata*, *I. forsteni*)

Kinixys Bell, 1827 (*K. belliana*, *K. erosa*, *K. homeana*, *K. natalensis*)

Malacochersus Lindholm, 1929 (*M. tornieri*)

Manouria Gray, 1852 (*M. emys*, *M. impressa*)

Psammobates Fitzinger, 1835 (*P. geometricus*, *P. oculifera*, *P. tentorius*)

Pyxis Bell, 1827 (*P. arachnoides*, *P. planicauda*)

Stigmochelys Gray, 1873 (*S. pardalis*)

Testudo Linnaeus, 1758

Testudo (*T. (T.) graeca*, *T. (T.) hermanni*, *T. (T.) kleinmanii*)

Agriemys Khozatsky & Mlynarski, 1966 (*T. (A.) horsfieldi*)

Biogeography

All recent testudinid phylogenies (e.g. Bour 1984; Crumly 1985; Gaffney & Meylan 1988) describe a vicariant biogeographical pattern with an early division between Gondwanan and Laurasian forms. These require the wide distribution and divergence of testudinids in the Cretaceous although the fossil record suggests a more recent origin for testudinids.

None of the existing testudinid phylogenies receives much support from

the fossil record. Testudinid fossils are unknown before the Eocene and even then are mostly restricted to shells (often fragmentary). These have been ascribed to several genera but all are poorly defined. The earliest testudinids are known from the early Eocene (Auffenberg 1974). During the Eocene Asia was connected to North America, with a narrow land bridge from North America through Greenland and Europe. Africa, Madagascar, India and South America were all isolated. During the Eocene there appear to have been several Asiatic genera, many now extinct. Forms resembling *Manouria* were found in all the northern continents whilst *Geochelone* (sensu lato) was restricted to Africa and several species of *Testudo* are recorded from Europe, Asia and Africa. These generic placements must be considered cautiously as *Manouria* is generally accepted to be plesiomorphic and the fragmentary remains of 'Manouria' may simply refer to large, poorly defined tortoises or large batagurids. 'Geochelone' and 'Indotestudo' are similarly poorly defined in most cases. The majority of fossil 'Testudo' need to be re-evaluated in a phylogenetic context. The only exceptions to this unreliable generic placement of fossil forms are the well defined *Gopherus*-like genera from North America (*Stylomys*, *Hesperotestudo* and *Xerobates*). The fossil data overall are too fragmentary, poorly defined and temporarily restricted to provide more than general support for any phylogeny or evolutionary scenario.

The present phylogeny suggests a strong influence of dispersal between the continents and allows for the evolution of the family in the Eocene. Recent testudinids appear to be descended from a northern taxon resembling *Manouria*). This taxon appears to have diverged into two main clades; the larger African and Malagasy clade and the American and small Old World forms. The former results from invasion of Africa during the mid-late Eocene taxa. Similarly invasion of India and adaptation to relatively dry forest habitats results in *Geochelone* sensu stricto. Colonisation of North America through the Thule connection with Europe results in the *Gopherus* and closely related fossil forms. *Chelonoidis* results from subsequent invasion of South America in the Miocene. Dispersal westwards and colonisation of Europe and Africa resulted in the evolution of *Indotestudo*, the European Mediterranean *Testudo* and the smaller African genera. Subsequent fragmentation of this continental group results in divergence of the western hemisphere and Eurasian taxa.

The African large tortoise clade divides on a geographical basis possibly as a result of a combination of dispersal and genetic drift. The base of this is the west African desert species *Centrochelys sulcata*, the east African population (*Stigmochelys pardalis*) colonised the islands of the western Indian Ocean giving rise to *Dipsoschelys*, 'Astrochelys', *Cylindraspis* and *Pyxis*. Divergence times for these taxa have been calculated (Caccone *et al.* 1999); giving the separation of the Malagasy tortoises from *Stigmochelys* (and by inference *Dipsoschelys*) at 14-22MYA, cladogenesis within the Malagasy taxa is suggested to have started 13-20MYA with the separation of *Pyxis* from 'Astrochelys' (and by inference *Cylindraspis*). *Pyxis arachnoides* and *P. (Acinyxis) planicauda* separated 8-12MYA as did *A. radiata* and 'A. yniphora'.

The small European and African taxa (*Cherisne angulata*, *Kinyxis* spp.,

Psammobates spp., *Homopus* spp., *Malacochersus tornieri* and *Testudo* spp.) may have diverged following habitat specialisation and Pleistocene habitat fragmentation. The *Chersina* + *Kinyxis* clade is generally forest or scrub inhabiting, whilst the remaining taxa inhabit semi-arid areas. Within *Homopus* + *Psammobates* + *Malacochersus* + *Testudo* there is a geographical division between the southern African *Psammobates* + *Homopus*, east African *Malacochersus* and Mediterranean *Testudo*, suggesting that these taxa diverged allopatrically; the complex biogeography of southern and eastern Africa would have provided isolating mechanisms in the form of rivers, mountains and deserts sufficient to separate the present-day genera.

Acknowledgements

I am grateful to N. Arnold, R. Bour, J. Pickering and R. Symmonds for allowing me to examine material in the BM(NH), MNHN, OUM and UMZ respectively and to B. Beckett, S. Tolan and R. Woodroffe for access to material in their private collections. P. Michaels and B. van Tiguel provided particularly useful specimens of *Geochelone elegans*.

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Appendix I. States of characters used in the cladistic analysis

Character	----- 11111111122222222233333333344444444455555555566666666
	123456789012345678901234567890123456789012345678901234567890123456
<i>Batagur</i>	000000000100000110100110001111000010111001000100100000010110101010
<i>Heosemys</i>	000000100100000111100110001011000001110001000100100000010110101010
<i>Manouria</i>	000000100100000100100010001010000100010001100100000000101010101011
<i>Centrochelys</i>	010101100100000110000010001000000000000101110100100100010110000000
<i>Stigmochelys</i>	110111100100001100100010011100000000011001110100000101010010010000
<i>Dipsochelys</i>	11011110000000110010001100100000000000001110101100000010000010000
<i>Acinyxis</i>	01011110010000111111101100100000010000000100000010010001010011000
<i>Pyxis</i>	010111100100001111111011001000000010000000100000010010001010011000
<i>'Astrochelys' yniphora</i>	010111100001011110100011001000000101000011110100010011010010010000
<i>Astrochelys radiata</i>	010111100000011110100011001000000001102010110100111011010010010000
<i>Cylindraspis</i>	010111100001011100100011000000000100102011110101011001000010010000
<i>Geochelone</i>	00000020010000111100001100100000000000000100100000100000111010001
<i>Gopherus</i>	001000211210100011100011001000111100101000100000021100100110000000
<i>Xerobates</i>	001000211210100011100011001000111100101000100000021100100110000000
<i>Chelonoidis</i>	000000201200000000100011000000000000001000100000100010000111010000
<i>Indotestudo</i>	000001201100000001101010001000000001000000100110000000000010010000
<i>Kinixys</i>	00000120110000000110111011100000000000010010000000000001010010101
<i>Chersina</i>	000001201100000001101110111100000001000100100010000000001010010101
<i>Psammobates</i>	00000120110000000110100001100000000000000100000100000010110010100
<i>Homopus</i>	00000120110000000110100011100000000000000100000100000011110010100
<i>Malacochersus</i>	000001201100000001001011011100000001001001001000000000010110010100
<i>Testudo</i>	00000120010000000110101111000000001001000001000130000000110010100
<i>Pseudotestudo</i>	000001200100000001101011111000000001001000001000130000000110010100
<i>Agrionemys</i>	000001200100000001100011111000000001000000001000130000010100010100

Appendix II The status of *Aldabrachelys* Loveridge & Williams, 1957

The first available name for the Seychelles-Madagascar group of giant tortoises is *Aldabrachelys* Loveridge & Williams, 1957. The diagnosis of *Aldabrachelys* would include all Seychelles-Madagascar giant tortoises although only the Aldabra atoll population was specified (as *Testudo gigantea* Schweigger, 1812). Subsequently the name was largely disregarded and in 1983 *Dipsochelys* was proposed as a full genus name for all Seychelles-Madagascar giant tortoises (Bour, 1983). Technically *Aldabrachelys* must be based on the type specimen of its type species. As this was specified as *G. gigantea*, it is based on the type of this species. Unfortunately, *G. gigantea* is not a Seychelles-Madagascar tortoise. Although its type specimen is lost the original description does not apply to any Seychelles-Madagascar species, being referable either to a Mascarene *Cylindraspis* (Bour 1984) or the South American *Chelonoidis denticulata* (Pritchard 1986). As noted by Bour (1983), under the International Code of Zoological Nomenclature operative at the time (2nd edition, operative 1974-1985) *G. gigantea* is not a valid name for the Aldabra tortoise and consequently *Aldabrachelys* must be considered a *nomen nudum*. Bour's definition of *Dipsochelys* has a valid type species and specimen and is technically correct under ICZN rules.

Table I. Names for the Aldabra tortoise - number of citations, with number of authors in parentheses*

	<1850	1851-1900	1901-1925	1926-1950	1951-1960	1961-1970	1971-1980	1981-1990	>199	total
species										
<i>indica</i>		2 (1)	0	0	0	0	0	0	0	2
<i>dussumieri</i>		1 (1)	0	0	0	0	0	0	0	16 (6)
<i>elephantina</i>		1 (1)	12 (5)	6 (2)	1 (1)	0	0	1 (1)	11 (5)	4 (3)
<i>gigantea</i>		1 (1)	7 (6)	5 (5)	3 (3)	9 (8)	8 (5)	35 (23)	39 (9)	3 (5)
<i>ponderosa</i>		0	1 (1)	0	0	0	0	0	0	0
<i>hololissa</i>		0	1 (1)	0	0	0	0	0	0	0
<i>sumeirei</i>		0	1 (1)	0	0	0	0	0	0	0
<i>daudinii</i>		0	2 (2)	2 (1)	0	0	1 (1)	0	0	0
<i>gouffeii</i>		0	0	2 (1)	0	0	0	0	0	0
<i>emys</i>		0	0	0	0	0	1 (1)	0	0	0
total		5	24	15	4	9	10	36	50	22
generic										
<i>Aldabrachelys</i>		0	0	0	0	1 (2)	0	0	0	1 (2)
<i>Dipsochelys</i>		0	0	0	0	0	0	0	11 (5)	20 (9)
<i>Geochelone</i>		0	0	0	0	0	5 (3)	33 (21)	39 (9)	2 (5)
<i>Megalochelys</i>		0	0	0	0	0	0	1 (1)	0	0
<i>Testudo</i>		5 (3)	24 (6)	15 (9)	4 (4)	8 (6)	5 (4)	2 (1)	0	0
total		5	24	15	4	9	10	36	50	22

*(from Stoddart 1997, updated with Satyamurti 1962; Pritchard 1979, 1988; Pritchard & Trebbau 1984; Alderton 1988; Ernst & Barbour 1989; King & Burke 1989; Broadley & Howell, 1991; Iverson 1992; Bour, 1994; Casares *et al.* 1995; Gerlach & Canning 1995, 1996; Gerlach 1997a-b, 1998a & b, 1999a-e, 2001; Devaux 1997 & 1999; Shahet *et al.* 1997; Bruekers 1998; Cooper 1998; Bourn *et al.* 1999; Ernst *et al.* 1999; Meylan & Sterrer 2000; Davenport 2001).

There has been some reluctance to adopt *Dipsochelys* and *Aldabrachelys* is still occasionally cited on the basis that '*Geochelone gigantea*' remains the more frequently used name and that conserving *gigantea* would promote stability. This could also validate *Aldabrachelys*. However, the perception that *gigantea* remains the most frequent name is not borne out by an examination of recent literature (Table I) which shows that the dominance of *gigantea* arose from the intense research on Aldabra in the 1970-80s, since then its use has fallen off significantly, forming only 14% of citations in the last decade.

Suggestions that the current edition of the ICZN (ICZN 1999) would validate the use of *Aldabrachelys* by interpreting the name as intended by Loveridge & Williams (1957) overlooks the fact that nomenclatural changes can only be judged by the edition in force at the time. Accordingly the actions of Bour (1983) in creating *Dipsochelys* were justified under the ICZN of the time and cannot be undone by the current edition. Thus the correct name for the Seychelles-Madagascar giant tortoise remains *Dipsochelys*.

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