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ScienceDirect

Zoology 110 (2007) 298–307

ZOOLOGY

www.elsevier.de/zool

When genes meet nomenclature: Tortoise phylogeny and the shifting generic concepts of *Testudo* and *Geochelone*

Uwe Fritz[a,*], Olaf R.P. Bininda-Emonds[b]

[a]*Museum of Zoology, Natural History State Collections Dresden, A.B. Meyer Building, D-01109 Dresden, Germany*
[b]*Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Erbertstrasse 1, D-07743 Jena, Germany*

Received 14 December 2006; received in revised form 8 February 2007; accepted 9 February 2007

Abstract

We used a five-gene data set (mtDNA: 12S rRNA, 16S rRNA, cyt-*b*; nDNA: Cmos, Rag2) comprising approximately two-thirds of all extant testudinid species and, for the first time, including all five *Testudo* species to investigate the question of whether all western Palaearctic testudinids are monophyletic. Further, we examined whether the recently suggested allocation of the African *Geochelone pardalis* in the otherwise exclusively South African genus *Psammobates* and of the Malagasy *G. yniphora* in the monotypic genus *Angonoka* is justified in the face of considerable morphological evidence against such placements. Our phylogenetic analyses do not support the paraphyly and generic break-up of *Testudo*, as suggested by previous papers using a smaller taxon sampling and mtDNA data only. We propose a continued usage of the generic name *Testudo* for all five western Palaearctic tortoise species. Within *Testudo*, two monophyletic subclades are present, one containing *T. hermanni* + *T. horsfieldii*, and the other comprising (*T. kleinmanni* + *T. marginata*) + *T. graeca*. Nomenclaturally, we demonstrate that *Eurotestudo* Lapparent de Broin et al., 2006, which was recently erected with the type species *T. hermanni*, is an objective junior synonym of *Chersine* Merrem, 1820 and *Medaestia* Wussow, 1916. Recognition of a monotypic genus *Angonoka* for *G. yniphora* is unwarranted according to both our re-analysis of sequence data and morphological data. Acknowledging the strong morphological similarity between *G. yniphora* and *G. radiata*, we suggest placing both species into the genus *Astrochelys*. Although sequence data for only one of the three *Psammobates* species was available for analysis, there is currently no cause to challenge the monophyly of this genus as established on the basis of morphological evidence. Thus, we hypothesize that *G. pardalis* is sister to a monophyletic *Psammobates*. In light of the clear morphological gap between *G. pardalis* and *Psammobates* species, the recognition of a distinct genus *Stigmochelys* for the former seems justified.

Keywords: Testudines; *Astrochelys*; *Geochelone*; *Stigmochelys*; *Testudo*

Introduction

Although chelonians are a small (less than 300 species; Ernst et al. 2000) and well-researched group, their taxonomy and systematics remain far from being well-understood. The genus *Testudo* Linnaeus, 1758 and

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*Corresponding author. Tel.: +49 351 8926 325.
E-mail address: uwe.fritz@snsd.smwk.sachsen.de (U. Fritz).

0944-2006/$ - see front matter © 2007 Elsevier GmbH. All rights reserved.
doi:10.1016/j.zool.2007.02.003

the family Testudinidae serve as cogent examples. *Testudo* was erected by Linnaeus (1758) to contain all chelonian species known to him, and was confined thereafter to true tortoises (e.g., Fitzinger 1826; Boulenger 1889; Siebenrock 1909; Williams 1952; Mertens and Wermuth 1955), thereby comprising the majority of the approximately 50 species (Ernst et al. 2000) currently constituting the family Testudinidae. The influential revision by Loveridge and Williams (1957) further restricted *Testudo* to only the five western Palaearctic tortoise species (*T. graeca*, *T. hermanni*, *T. horsfieldii*, *T. kleinmanni*, *T. marginata*), with the remaining species from other zoogeographic regions being assigned to distinct genera; many large-sized tropical tortoises were transferred into the genus *Geochelone*. A few years later, Khozatsky and Młynarski (1966) proposed another new genus, *Agrionemys*, for the Central Asiatic species *T. horsfieldii*. The generic distinctness of *T. horsfieldii* was accepted by a small number of authorities only (e.g., Chkhikvadze 1983, 1989; Obst 1985; Parham et al. 2006); most continued to treat it as a species of *Testudo* (e.g., Wermuth and Mertens 1977; Bour 1980; Crumly 1985; Ernst et al. 2000; Fritz and Cheylan 2001; Fritz et al. 2005, 2006, 2007; Le et al. 2006). A few palaeontological investigations transferred the extant northern Mediterranean *T. hermanni* into either *Agrionemys* (Gmira 1993a, b, 1995) or *Protestudo* Chkhikvadze, 1970 (Chkhikvadze 1983), the latter of which also includes several extinct species. Lapparent de Broin et al. (2006) described a new genus, *Eurotestudo*, to include some fossil species, the extant *T. hermanni* and two additional extant species, "*Testudo boettgeri*" and "*Testudo hercegovinensis*" that are typically viewed as being conspecific with *T. hermanni* (e.g., Fritz et al. 2006).

Although molecular genetic methods have proven to be a powerful tool for revealing phylogeography and species borders within *Testudo* (Fritz et al. 2005, 2006, 2007; Široký and Fritz 2007), they have at the same time considerably increased the number of contradicting phylogenetic hypotheses. For instance, 12S rRNA data proposed *Testudo* as being paraphyletic with respect to certain tropical testudinids (*Indotestudo elongata*, perhaps also *Geochelone carbonaria*, *G. denticulata*, *G. pardalis*, *G. sulcata*; van der Kuyl et al. 2002). Based on sequence data of the complete mitochondrial genome, however, Parham et al. (2006) did not support a paraphyletic *Testudo* with respect to *G. pardalis*; other *Geochelone* species were not studied. Instead, Parham et al. (2006) found, with weak statistical support, *T. hermanni* + *T. horsfieldii* to be the sister-group of a clade comprising the African *Malacochersus tornieri* and *Indotestudo elongata* + *I. forstenii* from Southeast Asia, whereas *T. graeca* + (*T. kleinmanni* + *T. marginata*) were strongly supported as the sister-group to all other species. By contrast, a third investigation (Le et al. 2006) of all extant testudinid genera using three mitochondrial (12S rRNA, 16S rRNA, cyt-*b*) and two nuclear genes (Cmos, Rag2) found *T. horsfieldii* + (*T. kleinmanni* + *T. graeca*) to be monophyletic, with *M. tornieri* and *Indotestudo* forming the sister-taxa, either as successive sister-taxa or as a monophyletic clade. Unfortunately, *T. hermanni* and *T. marginata* were not studied.

In the present study, we expand the five-gene dataset of Le et al. (2006) to include sequence information for the two *Testudo* species (*T. hermanni*, *T. marginata*) that were lacking in that study, with the goal of answering several outstanding points of contention within the genus. First, we examine whether or not the five western Palaearctic testudinids are monophyletic. Second, and more specifically, we address the question of whether or not *T. hermanni*, one of the best known and most frequently cited tortoise species of the world, should be placed in a distinct genus. Finally, we examine whether or not the suggestions of Le et al. (2006) to place the African *Geochelone pardalis* in the otherwise exclusively South African genus *Psammobates,* and *G. yniphora* in the monotypic genus *Angonoka* is justified in the face of considerable morphological evidence against such placements.

Material and methods

We supplemented the Le et al. (2006) five-gene molecular data set (12S rRNA, 16S rRNA, Cmos, cyt-*b*, Rag2) with homologous sequence data for *Testudo hermanni* and *T. marginata*. For the latter two species, we used two previously published cyt-*b* sequences (accession numbers AJ888319, AM230515; Fritz et al. 2005, 2006) and produced the other sequences (accession numbers AM491031–AM491038) in-house at the Museum of Zoology, Dresden using an ABI 3130 sequencer and the primers and lab procedures of Le et al. (2006). All five gene sequences derive from a single individual each of *T. hermanni* and *T. marginata*. Accession numbers for all sequences used from Le et al. (2006) are listed in that paper. The 12S rRNA sequence (accession number AF175336) labelled by Le et al. (2006) as being for *Geochelone chilensis* was removed from our analysis since it was originally described as coming from *G. denticulata* (van der Kuyl et al. 2002) and therefore is of uncertain provenance.

Alignments for each gene were obtained using either MUSCLE (Edgar 2004) for both 12S and 16S rRNA or transAlign (Bininda-Emonds 2005) in combination with ClustalW (Thompson et al. 1994) for the remaining, protein-coding genes, and improved by eye where necessary. None of the genes possessed any extremely hypervariable regions or other regions of questionable alignment. The final alignment comprised 3393 bp, of

Table 1. Sequence lengths for each gene

Gene	Aligned length	Number of characters (bp)		
		Constant	Informative	Uninformative
12S rRNA	411	255	116	40
16S rRNA	586	383	154	49
Cmos	602	492	61	49
Cyt-*b*	1140	527	479	134
Rag2	654	564	44	46
Supermatrix	3393	2221	854	318

which 2221 were constant across all taxa and 854 were parsimony informative (Table 1).

For the phylogenetic analyses, the individual data sets were concatenated into a single supermatrix (*sensu* Sanderson et al. 1998) and analyzed using a variety of methods: unweighted maximum parsimony (MP), the distance-based methods neighbour joining (NJ) and minimum evolution (ME), and the likelihood-based methods maximum likelihood (ML) and Bayesian analysis (BA). MP analyses were performed using PAUP* v4.0b10 (Swofford 2002) using a heuristic search strategy with a random-addition sequence, 10,000 replicates, steepest descent turned on, and a maximum of 10,000 equally optimal trees being saved. Both NJ and ME analyses also used PAUP* using GTR distances with a gamma correction. The latter model was chosen on the basis of MrAIC + PHYML (Guindon and Gascuel 2003; Nylander 2004) indicating a GTR + I + G model being optimal for the supermatrix. ME analyses used a heuristic search strategy with steepest descent turned on and a maximum of 10,000 equally optimal trees being saved. ML analyses used the default search parameters in RAxML VI-HPC v2.2.0 (Stamatakis 2006) with 25 replicates. A GTR + G model was assumed for the data, with the model parameters being allowed to vary independently for each gene. Support for the resulting topologies in each case was obtained using the bootstrap (Felsenstein 1981) with 1000 replicates and search parameters matching those for the optimality search. The only exception for the latter was for the MP analyses, where only 100 random-addition replicates were used within each bootstrap replicate. The resulting bootstrap values for the optimal solutions (or consensus thereof when numerous equally optimal solutions were obtained) were placed on the appropriate tree using the Perl script BootStrip. BA used MrBayes v3.1.2 (Ronquist and Huelsenbeck 2003). Analogous to the ML analyses, a GTR + I + G model was applied across the data set, but with parameters being able to vary between the different genes. Searches employed a MCMC algorithm with four chains that were run for 100,00,000 generations with the first 5,000,000 generations being discarded as burn-in. Trees were sampled every 5000 generations to derive the final tree and estimates of the posterior probabilities. In all cases, trees were rooted using an outgroup comprising *Deirochelys reticularia*, *Glyptemys insculpta*, *Rhinoclemmys melanosterna* and *Rhinoclemmys nasuta*; these taxa have been removed from all trees presented in Fig. 1 for clarity.

The final data matrix and all inferred phylogenetic trees (including outgroup taxa) are freely available from TreeBASE (Sanderson et al. 1994; www.treebase.org) under the study accession number S1712 and matrix accession number M3100. For space considerations, the NJ and ME trees are only available on TreeBASE.

Results

Our expanded data set of all western Palaearctic tortoise species did not alter the general framework established by Le et al. (2006). Differences are limited largely to the positions of the monotypic African genus *Malacochersus*, the three Asiatic *Indotestudo* species, and the Malagasy *Geochelone yniphora*. The polyphyly of *Geochelone sensu lato* is well-supported under all of our phylogenetic analyses, suggesting that the taxonomic revision proposed by Le et al. (2006) is generally appropriate.

All tree-building methods reveal *Malacochersus*, *Indotestudo* and the western Palaearctic *Testudo* species to be a monophyletic clade with bootstrap or posterior probability values of 99/0.99 or greater. Relationships within this clade, however, differ between the different methods. The only strongly supported clades are that of *Indotestudo* species and (*Testudo kleinmanni* + *T. marginata*) + *T. graeca*. Both distance-based analyses hold *Malacochersus* to be the sister-taxon of a weakly supported clade containing *Indotestudo* and *Testudo* (bootstrap values of 34 and 48 for ME and NJ, respectively); MP, ML and BA suggest instead a sister-group relationship between a weakly supported clade comprising *Malacochersus* + *Indotestudo* and a moderately supported clade containing all *Testudo* species

(Figs. 1a–c). The monophyly of (*T. kleinmanni* + *T. marginata*) + *T. graeca* is well-supported by each of the three latter methods; this clade is sister to a weakly (MP) to moderately well-supported clade (ML, BA) of *T. hermanni* and *T. horsfieldii*.

The phylogenetic resolution of our strict consensus of 774 equally parsimonious trees is much worse than that found by Le et al. (2006); many taxa appear in an unresolved comb (strict consensus available from TreeBASE only; see also percentages in Fig. 1a). In contrast to the MP analysis of Le et al. (2006), *Geochelone yniphora* is not sister to a clade containing the other Malagasy species (*Pyxis* spp. and *G. radiata*) and the Indian Ocean giant tortoises (*Aldabrachelys gigantea*) in our MP analysis. A 50% majority rule consensus, however, reveals *G. yniphora* as being sister to the weakly supported clade of *G. radiata* + (*Pyxis arachnoides* + *P. planicauda*); this purely Malagasy clade, in turn, constitutes the sister-group of the Indian Ocean *A. gigantea*. The branching pattern in the ME and NJ trees perfectly

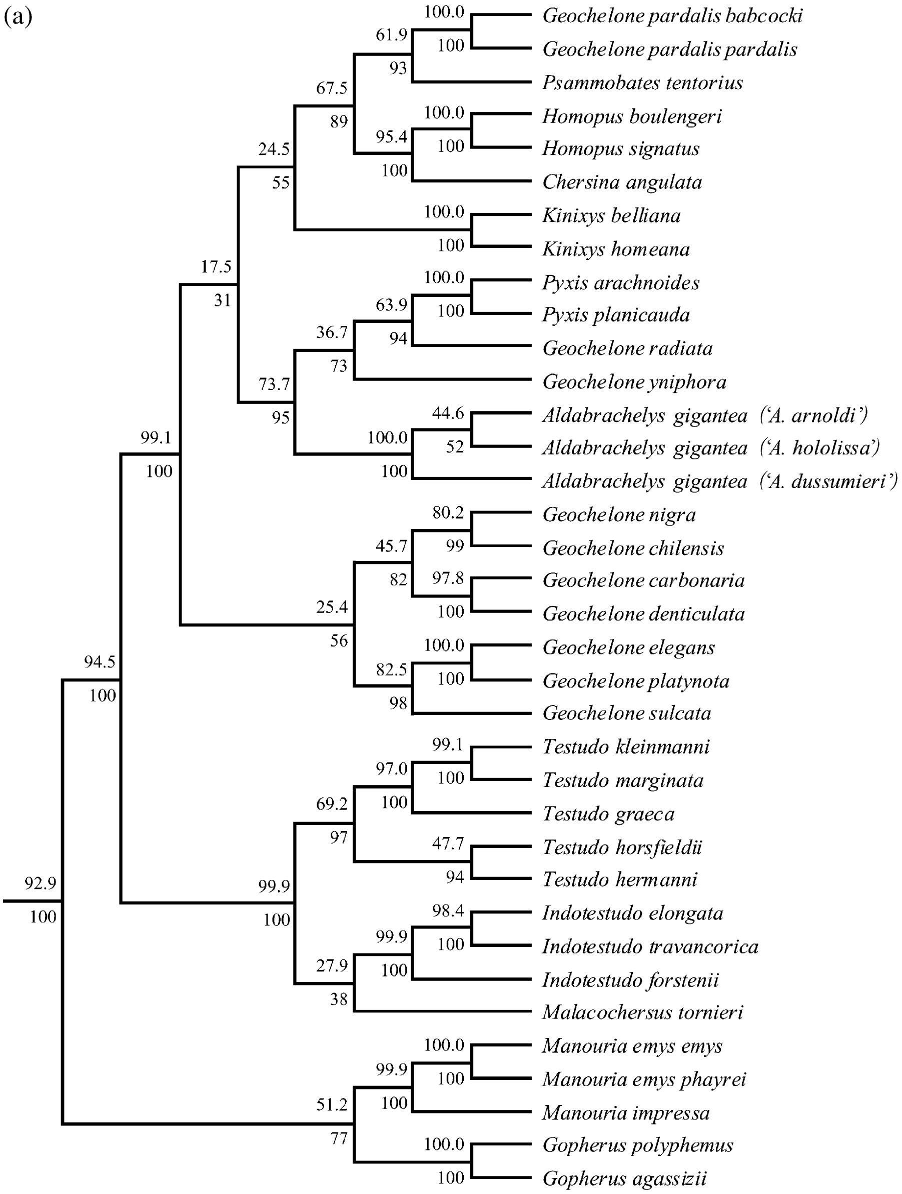

Fig. 1. Phylogenetic relationships within Testudinidae as revealed by analysis of a multigene data set using (a) MP, (b) ML, and (c) BA. For all trees, support values for each clade (MP and ML, bootstrap; BA, posterior probabilities) are given. The MP tree is a majority-rule consensus of 774 equally parsimonious trees; the frequency of occurrence for each clade appears below its respective node. Branch lengths for the ML and BA trees are proportional to the mean number of substitutions per site; branch lengths for the MP tree are arbitrary. Species names applied to *Aldabrachelys gigantea* sequences by Le et al. (2006) are presented in brackets (for usage of the name *A. gigantea*, see Frazier 2006a, b).

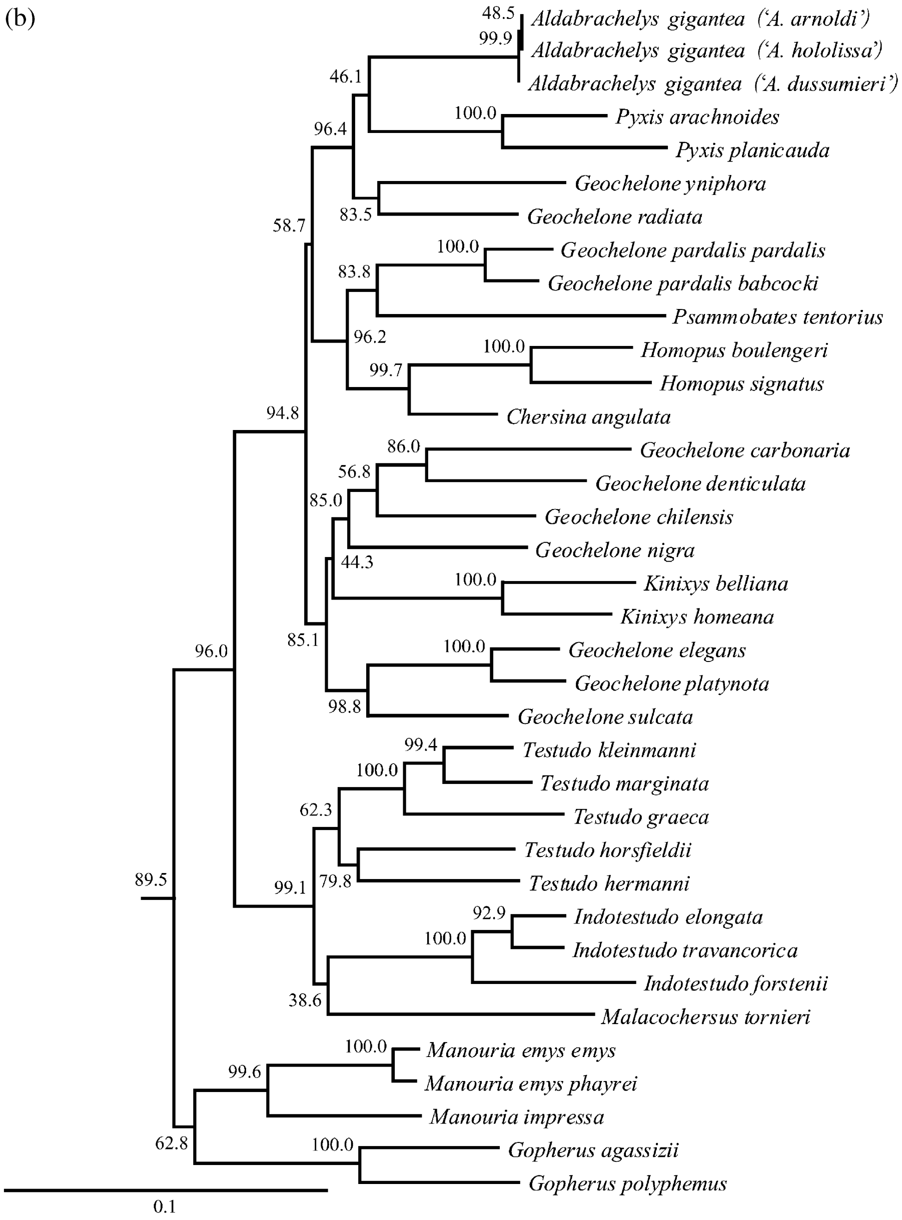

Fig. 1. (*Continued*)

matches the tree topology of the MP tree presented by Le et al. (2006) in that *G. yniphora* is basal to all other Malagasy taxa plus *A. gigantea*; however, the monophyly of the clade comprising (*G. radiata* + (*P. arachnoides* + *P. planicauda*)) + *A. gigantea* is decidedly weak (ME: 49; NJ: 62). The remaining phylogenetic analyses place *G. yniphora* consistently and with high support (ML: 84, BA: 1.0) as the sister-taxon of *G. radiata*.

The 50% majority rule MP consensus tree as well as all other tree-building methods all indicate *Psammobates tentorius* to be the sister-taxon of the two *G. pardalis* subspecies, statistical support for this *Psammobates* + *G. pardalis* clade is weak (ME: 66; MP: 62; NJ: 66) to high (ML: 84; BA: 1.0).

Discussion

Are western Palaearctic tortoises monophyletic and which generic name(s) should be applied?

Our results, based on sequence data for three mitochondrial and two nuclear genes of approximately two-thirds of all extant testudinid species and all five *Testudo* species, do not support the paraphyly of *Testudo*, as suggested by previous papers using a smaller taxon-sampling and mtDNA data only (van der Kuyl et al. 2002; Parham et al. 2006). The recognition of a distinct genus for *T. hermanni* (*Eurotestudo*), as suggested by Lapparent de Broin et al. (2006) is therefore

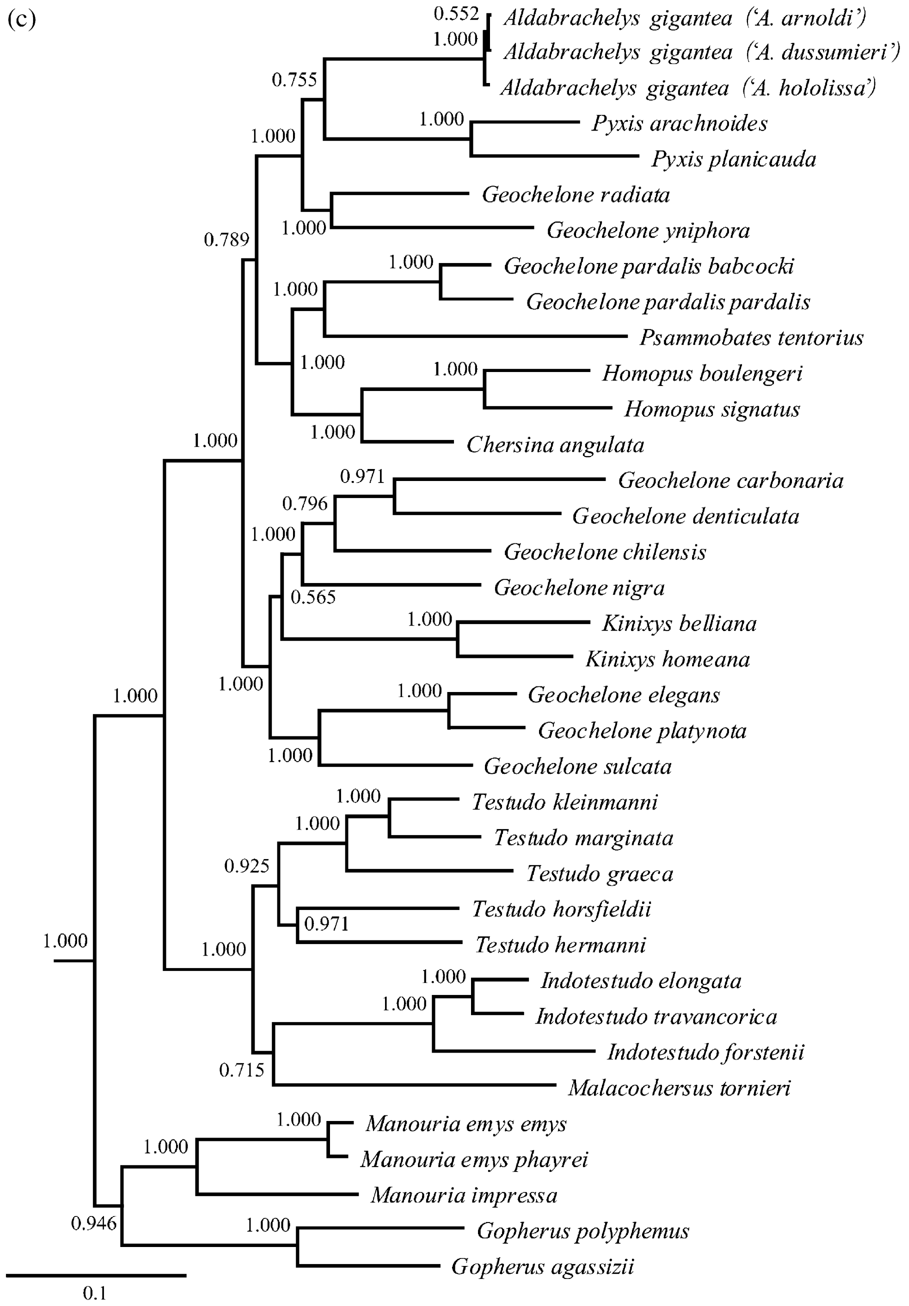

Fig. 1. (*Continued*)

not warranted on this basis. Moreover, *T. hermanni* clearly clusters with *T. horsfieldii*, with these two species constituting the sister-group of the other three western Palaearctic tortoise species. Therefore, if any nomenclatural distinction is to be made, we recommend treating the two former species as the distinct subgenus *Agrionemys* to avoid unnecessary name changes.

In support of erecting the new genus *Eurotestudo* (type species: *T. hermanni* Gmelin, 1789) in the face of two older names being available (*Chersine* Merrem, 1820 and *Medaestia* Wussow, 1916), Lapparent de Broin et al. (2006) claim that these latter names were based on the type species *T. graeca* Linnaeus, 1758 and, therefore, cannot be applied to *T. hermanni*. In so doing, Lapparent de Broin et al. (2006) have unfortunately added a further chapter to the complicated and confusing nomenclatural history of *Testudo*. The name *T. graeca* was misapplied for decades after its description by Linnaeus (1758) by virtually all subsequent authors (e.g., Schoepff 1792–1801; Hermann 1804; Merrem 1820; Fitzinger 1826; Gray 1844, 1870; Strauch 1862; Schreiber 1875; Lortet 1887; Boulenger 1889;

Siebenrock 1909), who used this name for the species now known as *T. hermanni* Gmelin, 1789. It was not until the early 20th century that Siebenrock (1913) and Flower (1925, 1926) recognized this error. Whereas Siebenrock (1913) hesitated to change the long-established usage of the name *T. graeca*, Flower (1925, 1926) pointed out that the name *T. graeca* has to be applied to the species previously known under the name of *T. ibera* Pallas, 1814 and that *T. hermanni* Gmelin, 1789, a name treated for more than a century as junior synonym of *T. graeca* Linnaeus, 1758, has to be used for what was known before as *T. graeca*. While later authors followed Flower's proposal, this situation still continues to cause major confusion and mixing-up of data for these two tortoise species, both of which are among the most frequently cited chelonian species of the world (e.g., in the years 2000 to 2005 inclusive, *T. hermanni* and *T. graeca* were mentioned in 121 and 102 publications, respectively, according to *Zoological Record*). As regards the names *Chersine* Merrem, 1820 and *Medaestia* Wussow, 1916, it is obvious from the period when they were proposed that they were based on the misapplication of the name *T. graeca* Linnaeus, 1758 and that actually *T. hermanni* was meant. In accordance with article 69.2.4 of the International Code of Zoological Nomenclature (ICZN 1999), both Lindholm (1929) and Mertens (1949) recognized and explicitly referred to this misapplication when they designated *T. hermanni* as the type species of *Chersine* and *Medaestia,* respectively. Consequently, *T. hermanni* is the valid type species of either name, rendering *Eurotestudo* Lapparent de Broin et al., 2006 an objective junior synonym of both.

A monotypic genus for *Geochelone yniphora* and should *G. pardalis* be placed into *Psammobates*?

Our re-analysis of the data of Le et al. (2006) generally corroborates their generic revision of *Geochelone sensu lato*, which is clearly polyphyletic. Therefore, we agree that the genus *Geochelone* Fitzinger, 1835 (type species: *G. elegans*) should be restricted to *G. elegans*, *G. platynota* (both from southern Asia) and *G. sulcata* (Africa). We further agree that all the South American *Geochelone* species (*G. carbonaria*, *G. chilensis*, *G. denticulata*, *G. nigra*) should be placed into the genus *Chelonoidis* Fitzinger, 1835 (type species: *C. carbonaria*).

However, we disagree with the assignment of the African *G. pardalis* to *Psammobates* (South Africa) in light of the generic arrangement proposed by Le et al. (2006) for the Malagasy–Indian Ocean tortoises *Aldabrachelys*, *Geochelone* and *Pyxis*. In each case, morphologically extremely divergent tortoises are involved. For instance, *G. pardalis* is a large-sized African tortoise, reaching a maximum shell length of approximately 70 cm, whereas the genus *Psammobates sensu stricto* comprises three small, exclusively South African species with a shell length of only approximately 15 cm (Ernst et al. 2000). A similar range of distinct size classes is present in the Malagasy–Indian Ocean taxa. The Indian Ocean genus *Aldabrachelys* comprises dark-coloured giant tortoises that represent only a single extant species (Austin et al. 2003; Palkovacs et al. 2003; Frazier 2006a, b), although the existence of up to three distinct species was recently claimed (Bour 1982; Gerlach and Canning 1998; Gerlach 2004). These giant tortoises are characterized by an unusual skull morphology (Bour 1982) and reach approximately 120 cm in shell length and more than 300 kg in weight. By contrast, the Malagasy species are much smaller and brightly coloured: *G. radiata* and *G. yniphora* are medium-sized with a highly domed shell (maximum shell length approx. 45 cm) and *Pyxis arachnoides* and *P. planicauda* are small tortoises with an elongated shell (maximum shell length approx. 15 cm; Ernst et al. 2000).

Yet, while Le et al. (2006) lump *G. pardalis* with *Psammobates*, they argue explicitly that similar morphological differences justify the recognition of distinct genera for the Indian Ocean and Malagasy tortoises. *Aldabrachelys* is retained for the Indian Ocean species and *Pyxis* for *P. arachnoides* and *P. planicauda*, with the Malagasy tortoises *G. radiata* and *G. yniphora* being placed into two distinct, monotypic genera (*Astrochelys* Gray, 1873 and the newly erected genus *Angonoka* Le et al., 2006, respectively). Although we agree with Le et al. (2006) that *G. pardalis*, *G. radiata* and *G. yniphora* should be removed from *Geochelone*, the justification for monotypic genera for the latter two species seems weak according to both our re-analysis of sequence data and morphological data. In agreement with the long-appreciated strong morphological similarity between *G. yniphora* and *G. radiata*, which prompted suggestions early in the 20th century that both are conspecific (Siebenrock 1909), both species appear as strongly supported sister-taxa in the BA and ML analyses (support values of 1.0 and 84, respectively). Under the other tree-building methods, the sister-group relationship between *G. yniphora* and other Malagasy or Indian Ocean plus Malagasy taxa is at best weakly supported. Therefore, to avoid two monotypic genera that are at best weakly supported, we suggest placing both *G. radiata* and *G. yniphora* into *Astrochelys* and treating *Angonoka* Le et al., 2006 (type species: *A. yniphora*) as a subjective junior synonym of *Astrochelys* Gray, 1873 (type species: *A. radiata*).

Although sequence data for only one of the three highly protected *Psammobates* species were available for analysis, there is currently no evidence to challenge the monophyly of this genus as established on the basis of morphological characters (Loveridge and Williams 1957). Thus, we hypothesize that *G. pardalis* is sister to a monophyletic *Psammobates*. In light of the clear morphological gap between *G. pardalis* and *Psammobates* spp., the recognition of a distinct genus for the former seems justified. Gerlach (2001) suggested placing *G. pardalis* into the genus *Stigmochelys* Gray, 1873 (type species: *S. pardalis*) based on morphological evidence and we concur that this nomenclatural arrangement provides the best current compromise of morphological distinctness and phylogenetic relatedness.

Conclusions

Using a five-gene data set consisting of three mitochondrial (12S rRNA, 16S rRNA, cyt-*b*) and two nuclear genes (Cmos, Rag2) and, for the first time, including all five western Palaearctic testudinid species, our phylogenetic analyses agree with the general findings of Le et al. (2006) that *Geochelone* is paraphyletic and should be split into several smaller units (Table 2). Our data further provide evidence for the monophyly of the genus *Testudo*. Considering that several species of *Testudo* are among the most frequently cited of all testudinid species and are of high relevance in nature conservation, the proposed changes to the generic names for some species (e.g., Khozatsky and Młynarski 1966; Chkhikvadze 1983; Gmira 1993a, b, 1995; Lapparent de Broin et al. 2006) are unwarranted for practical reasons in addition to being apparently unjustified scientifically. Moreover, our nomenclatural suggestions for the African as well as the Indian Ocean and Malagasy tortoise genera best reflect both the morphological distinctiveness and the phylogenetic relationships of the species involved.

Table 2. Recommended nomenclature for extant genera and species of Testudinidae, including taxa that have gone extinct in historical times

Aldabrachelys Loveridge & Williams, 1957
  †*Aldabrachelys abrupta* (Grandidier, 1868)
  Aldabrachelys gigantea (Schweigger, 1812)
  †*Aldabrachelys grandidieri* (Vaillant, 1885)

Astrochelys Gray, 1873
  Astrochelys radiata (Shaw, 1802)
  Astrochelys yniphora (Vaillant, 1885)

Chelonoidis Fitzinger, 1835
  Chelonoidis carbonaria (Spix, 1824)
  Chelonoidis chilensis (Gray, 1870)
  Chelonoidis denticulata (Linnaeus, 1766)
  Chelonoidis nigra (Quoy & Gaimard, 1824)

Chersina Gray, 1831
  Chersina angulata (Schweigger, 1812)

†***Cylindraspis*** Fitzinger, 1835
  †*Cylindraspis indica* (Schneider, 1783)
  †*Cylindraspis inepta* (Günther, 1873)
  †*Cylindraspis peltastes* (Duméril & Bibron, 1835)
  †*Cylindraspis triserrata* (Günther, 1873)
  †*Cylindraspis vosmaeri* (Fitzinger, 1826)

Geochelone Fitzinger, 1835
  Geochelone elegans (Schoepff, 1794)
  Geochelone platynota (Blyth, 1863)
  Geochelone sulcata (Miller, 1779)

Gopherus Rafinesque, 1832
  Gopherus agassizii (Cooper, 1863)
  Gopherus berlandieri (Agassiz, 1857)
  Gopherus flavomarginatus Legler, 1959
  Gopherus polyphemus (Daudin, 1801)

Table 2. (*continued*)

Homopus Duméril & Bibron, 1835
  Homopus areolatus (Thunberg, 1787)
  Homopus boulengeri Duerden, 1906
  Homopus femoralis Boulenger, 1888
  Homopus signatus (Gmelin, 1789)

Indotestudo Lindholm, 1929
  Indotestudo elongata (Blyth, 1853)
  Indotestudo forstenii (Schlegel & Müller, 1844)
  Indotestudo travancorica (Boulenger, 1907)

Kinixys Bell, 1827
  Kinixys belliana (Gray, 1831)
  Kinixys erosa (Schweigger, 1812)
  Kinixys homeana Bell, 1827
  Kinixys lobatsiana (Power, 1927)
  Kinixys natalensis Hewitt, 1935
  Kinixys spekii Gray, 1863

Malacochersus Lindholm, 1929
  Malacochersus tornieri (Siebenrock, 1903)

Manouria Gray, 1852
  Manouria emys (Schlegel & Müller, 1844)
  Manouria impressa (Günther, 1882)

Psammobates Fitzinger, 1835
  Psammobates geometricus (Linnaeus, 1758)
  Psammobates oculifer (Kuhl, 1820)
  Psammobates tentorius (Bell, 1828)

Pyxis Bell, 1827
  Pyxis arachnoides Bell, 1827
  Pyxis planicauda (Grandidier, 1867)

Stigmochelys Gray, 1873
  Stigmochelys pardalis (Bell, 1828)

Testudo Linnaeus, 1758
  Testudo graeca Linnaeus, 1758
  Testudo hermanni Gmelin, 1789
  Testudo horsfieldii Gray, 1844
  Testudo kleinmanni Lortet, 1883
  Testudo marginata Schoepff, 1792

Extinct taxa are indicated by a dagger (†) preceding their scientific names.

Acknowledgements

Thanks go to Otto Kraus (Zoological Institute and Museum, University of Hamburg) for helping to clarify the valid type species of *Chersine* and *Medaestia* and to Anke Müller (Museum of Zoology, Dresden) for lab work. OBE was supported by a Heisenberg Scholarship of the DFG (BI 825/2–1). George Zug and two anonymous reviewers made helpful comments on an earlier version of the manuscript. All Perl scripts mentioned are freely available at www.uni-jena.de/~b6biol2/.

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