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Competing generic concepts for Blanding's, Pacific and European pond turtles (*Emydoidea, Actinemys* and *Emys*)—Which is best?

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Abstract

We review competing taxonomic classifications and hypotheses for the phylogeny of emydine turtles. The formerly recognized genus *Clemmys* sensu lato clearly is paraphyletic. Two of its former species, now *Glyptemys insculpta* and *G. muhlenbergii*, constitute a well-supported basal clade within the Emydinae. However, the phylogenetic position of the other two species traditionally placed in *Clemmys* remains controversial. Mitochondrial data suggest a clade embracing *Actinemys* (formerly *Clemmys*) *marmorata*, *Emydoidea* and *Emys* and as its sister either another clade (*Clemmys guttata* + *Terrapene*) or *Terrapene* alone. In contrast, nuclear genomic data yield conflicting results, depending on which genes are used. Either *Clemmys guttata* is revealed as sister to ((*Emydoidea* + *Emys*) + *Actinemys*) + *Terrapene* or *Clemmys guttata* is sister to *Actinemys marmorata* and these two species together are the sister group of (*Emydoidea* + *Emys*); *Terrapene* appears then as sister to (*Actinemys marmorata* + *Clemmys guttata*) + (*Emydoidea* + *Emys*). The contradictory branching patterns depending from the selected loci are suggestive of lineage sorting problems. Ignoring the unclear phylogenetic position of *Actinemys marmorata*, one recently proposed classification scheme placed *Actinemys marmorata*, *Emydoidea blandingii*, *Emys orbicularis*, and *Emys trinacris* in one genus (*Emys*), while another classification scheme treats *Actinemys*, *Emydoidea*, and *Emys* as distinct genera. The inclusion of *Actinemys* in the same taxon as *Emydoidea* + *Emys* is unacceptable under a phylogenetic classification framework because there is evidence for the non-monophyly of this clade. Moreover, *Actinemys*, *Emydoidea*, and *Emys* are morphologically highly distinct. Their morphological divergence exceeds by far the differences that typically occur among species of the same genus, so that a continued usage of the distinct genera *Actinemys*, *Emydoidea* and *Emys* is recommended.

Key words: Classification, *Actinemys*, *Clemmys*, Emydidae, Emydinae, *Emydoidea*, *Emys*, *Glyptemys*, Testudines

Prologos

While for many decades the generic arrangement of American emydid turtles was stable (Loveridge & Williams 1957; Ernst & Barbour 1972, 1989; Wermuth & Mertens 1977; Ernst *et al.* 2000), with the notable exception of *Chrysemys*, *Pseudemys* and *Trachemys* (McDowell 1964; Seidel & Smith 1986), the situation changed in recent years with the advent of molecular phylogenetics. In the present paper we review competing phylogenetic hypotheses and the resulting contentious situation for genus delineation of the pond turtle complex (genera *Actinemys*, *Emydoidea*, and *Emys vs.* an expanded genus *Emys*). The problem of generic assignment of these turtles was first addressed by C. H. Ernst in a keynote lecture of a symposium on the former genus *Clemmys* at Pennsylvania State University in 2000 (Ernst 2001).

Parodos

The genus *Emys* (ancient Greek *έμύς*, freshwater turtle) was erected by André Marie Constant Duméril (1806) to comprise a wide variety of freshwater turtles. During the 19th century, about 90 extant and many additional fossil

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species were assigned to this genus, among them representatives of the families Chelidae, Chelydridae, Dermatemydidae, Emydidae, Geoemydidae, Kinosternidae, Pelomedusidae, Platysternidae, Podocnemididae, and Testudinidae (Fritz & Havaš 2007). Only in the late 19th century, the usage of *Emys* became increasingly restricted, and Boulenger (1889) placed only two species in this genus: *E. orbicularis* and *E. blandingii*, an arrangement that persisted until Loveridge & Williams (1957) transferred the latter species in the genus *Emydoidea*, acknowledging its highly divergent skull, neck and thoracic rib morphology which resembles that of *Deirochelys reticularia*. Many other species that were previously in *Emys* were later placed in the genus *Clemmys* Ritgen, 1828. This genus embraced for many years a number of Old and New World freshwater turtles (Wagler 1830; Strauch 1862; Boulenger 1889; Siebenrock 1909; Wermuth & Mertens 1961), mostly generalized species without any obvious morphological peculiarities. A prominent exception among the 19th century scholars was Louis Agassiz (1857), who treated each of the New World species assigned to *Clemmys* by contemporary authors as a representative of a distinct genus (*Actinemys marmorata*, *Calemys muhlenbergii*, *Glyptemys insculpta*, *Nanemys guttata*).

Epeisodion

After McDowell's (1964) pioneering osteological study revising the 'aquatic Testudinidae', *Clemmys* was restricted to the four Nearctic species *Clemmys guttata*, *C. insculpta*, *C. marmorata* and *C. muhlenbergii*, while the remaining Old World species were transferred to the genera *Mauremys* and *Sacalia*. McDowell (1964) discovered that most Old World and New World freshwater turtles represent highly distinct groups. Consequently, he placed all Old World species plus the extraterritorial Neotropical genus *Rhinoclemmys* in the subfamily Batagurinae and the New World species plus the Palaearctic genus *Emys* in the Emydinae. These two subfamilies constituted, along with land tortoises (Testudininae), the family Testudinidae in McDowell's (1964) classification. This general scheme currently stands, although each of these groups is now treated as a full family and the name Geoemydidae replaced Bataguridae because of priority reasons (Fritz & Havaš 2007; Rhodin *et al.* 2010). McDowell (1964) realized the close relationship of the four Nearctic *Clemmys* species, of *Terrapene* and the Old World species *Emys orbicularis*, all of which were placed by him in the '*Emys* complex'. Yet, McDowell (1964) did not include *Emydoidea blandingii* in this group, but in the distinct '*Deirochelys* complex', together with *Deirochelys reticularia*. In doing so, McDowell followed Loveridge & Williams (1957), acknowledging that the morphological similarity of skull, neck, and thoracic rib morphology of *Deirochelys* and *Emydoidea* reflects a close relationship.

However, as Bramble (1974) pointed out, the morphology of structures associated with the plastral hinge of *Emydoidea* argues rather for a close relationship of *Emydoidea* with *Emys* and *Terrapene*, and not with *Deirochelys*. The plastral hinge of *Emys*, *Emydoidea* and *Terrapene* consists of ligamentous tissue that constitutes a syndesmotic connection of carapace and plastron, but also between the hyo- and hypoplastral bones, enabling the mobility of both plastral lobes and more or less complete closure of the shell. Shell closure is most perfectly developed in *Terrapene* species (Fig. 1), as reflected, not least, by their common name 'box turtles'. Using Bramble's (1974) detailed description of the morphological structures associated with the plastral hinge, Gaffney & Meylan (1988) concluded that *Emys*, *Emydoidea* and *Terrapene* represent a monophyletic group within the subfamily Emydinae (as opposed to the subfamily Deirochelyinae within the family Emydidae). All three genera share not only a plastral hinge, but also the peculiar morphology of a divided scapula, a unique character among extant chelonians. *Emys* has a bipartite scapula, with a distinct distal bone element, the so-called suprascapula. In *Emydoidea* and *Terrapene* a third scapular bone, the episcapula, occurs that is located on the tip of the suprascapula (Fig. 2). The tripartite scapula of *Emydoidea* and *Terrapene* plays an important role in stabilizing the opened shell (Bramble 1974; see also Fig. 1). According to Gaffney & Meylan (1988), the suprascapula is a synapomorphy of *Emys*, *Emydoidea* and *Terrapene*, and the episcapula a synapomorphy of *Emydoidea* and *Terrapene* (Fig. 3: top left). The morphological similarity of these structures of *Emydoidea*, *Emys* and *Terrapene* is so compelling that Bramble (1974) concluded "A multiple origin for the complex closing mechanism held in common by these box turtles appears extremely remote".

Gaffney & Meylan (1988) believed that the four *Clemmys* species, lacking not only the plastral hinge, but also all of the complicated morphological structures associated with this character, have collectively a basal phylogenetic position within Emydinae (Fig. 3: top left), as implicitly already assumed by McDowell (1964) and explicitly by Bramble (1974). Gaffney & Meylan (1988) placed all other emydid genera (*Chrysemys*, *Deirochelys*, *Graptemys*, *Malaclemys*, *Pseudemys*, *Trachemys*) in another subfamily (Deirochelyinae) within the Emydidae. However, already previous and contemporary studies using morphological, cytosystematic and electrophoretic characters suggested that relationships within *Clemmys* sensu stricto are not straightforward (see the reviews in Lovich *et al.* 1991 and Ernst 2001).

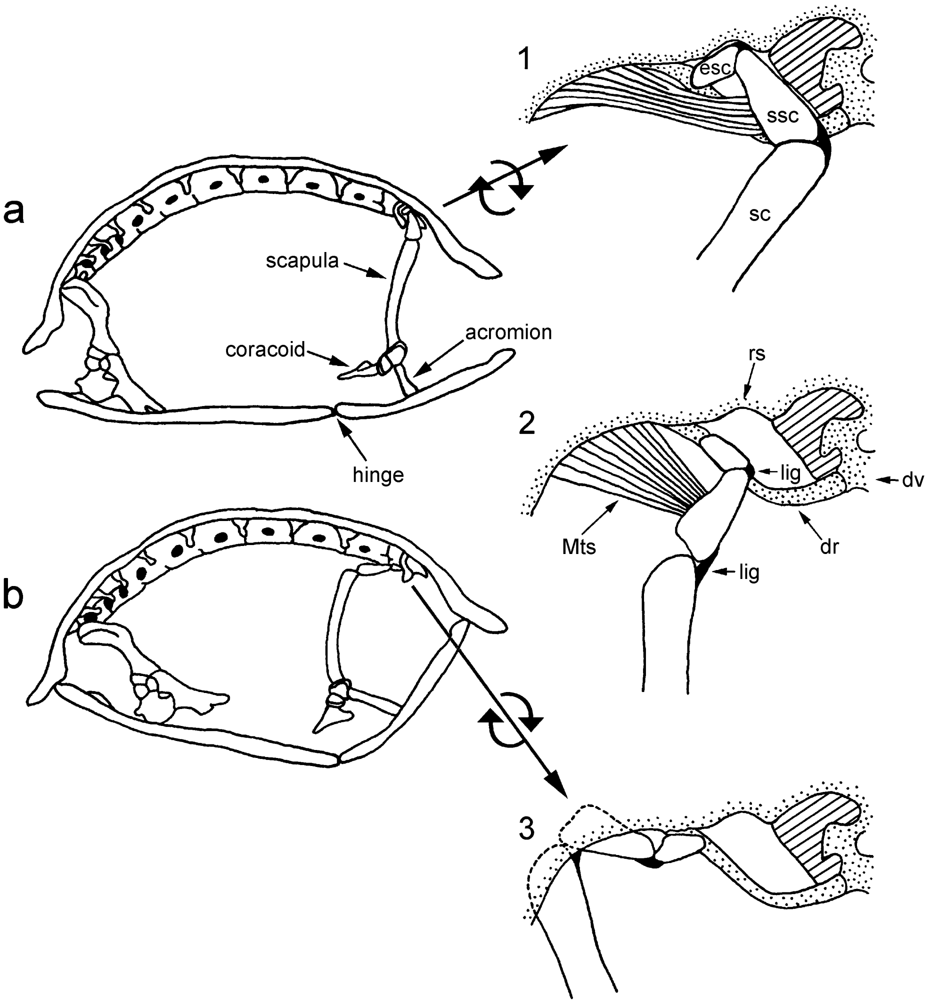

FIGURE 1. Longitudinal sections of a *Terrapene* shell (*left*) and cross sections of right scapulo-carapacial articulation of *Terrapene* (*right*) to demonstrate relationships between scapula and carapace when shell is open (a), corresponding to a 'locked' scapulo-carapacial articulation (1), and when shell is closed (b), corresponding to a disengaged scapulo-carapacial articulation (3). The *medial figure right* (2) shows the disengaging of the scapulo-carapacial articulation during shell closure. Abbreviations: *esc:* episcapula, *ssc:* suprascapula, *sc:* scapula, *rs:* recessus scapularis, *Mts:* Musculus testoscapularis, *lig:* ligament, *dr:* dorsal rib, *dv:* dorsal vertebra. Redrawn and modified from Bramble (1974); reproduction from Fritz (2003) with permission of Laurenti Verlag.

Later, the morphology-based phylogeny of emydine turtles of Gaffney & Meylan (1988) was not only challenged, but in part severely contradicted by molecular studies. Using sequences of the partial 16S rRNA gene, Bickham *et al.* (1996) suggested that the long-recognized genus *Clemmys* is paraphyletic with respect to all other genera of the subfamily Emydinae (*Emys*, *Emydoidea*, *Terrapene*; Fig. 3: top right). In their analyses, *Clemmys guttata* was sister to all other emydines. A clade comprising *C. insculpta* and *C. muhlenbergii* was the sister group to a major clade embracing a subclade with *Emys orbicularis*, *Emydoidea blandingii*, and *C. marmorata,* and another subclade with all studied *Terrapene* species as its sister group. This topology conflicted with the previous assumption that the genera with (*Emys*, *Emydoidea*, *Terrapene*) or without plastral hinge (*Clemmys*) constitute distinct groups (Bramble 1974; Gaffney & Meylan 1988). When Burke *et al.* (1996) combined the 16S rRNA data of Bickham *et al.* (1996) with evidence from morphology, behavior and life history, a topology resulted with the hinged taxa nested within *Clemmys* species (Fig. 3: bottom left). Based on these findings, Burke *et al.* (1996) considered expanding the genus *Emys* to include all emydine species except *C. insculpta* and *C. muhlenbergii*.

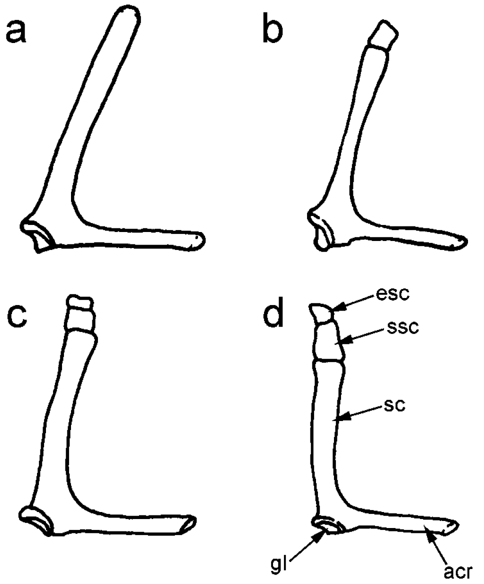

FIGURE 2. Anterior views of (a) the right scapula of emydine turtle with ancestral character state as occurring in *Actinemys*, *Clemmys*, and *Glyptemys* species, (b) bipartite scapula of *Emys*, (c) tripartite scapula of *Emydoidea*, and (d) tripartite scapula of *Terrapene*. Abbreviations: *esc:* episcapula, *ssc:* suprascapula, *sc:* scapula, *gl:* glenoid, *acr:* acromion. Redrawn from Bramble (1974); reproduction from Fritz (2003) with permission of Laurenti Verlag.

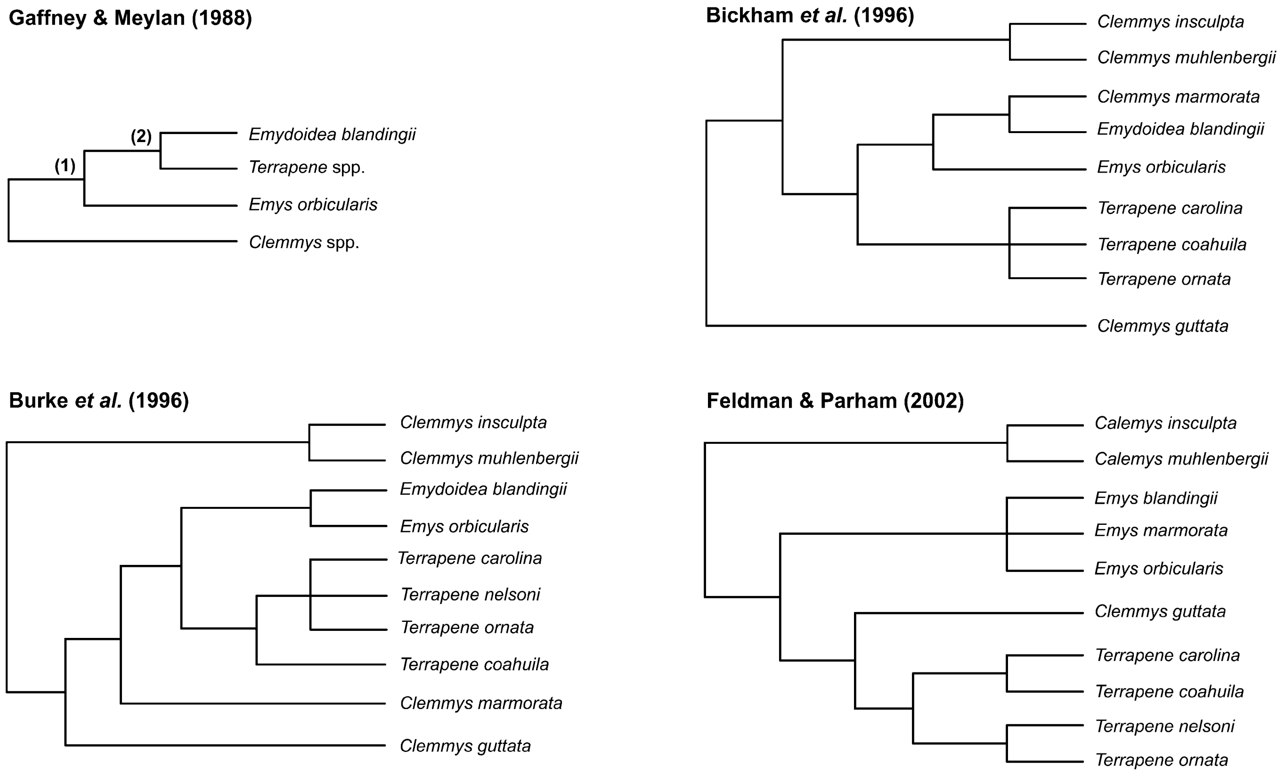

FIGURE 3. Phylogenetic hypotheses for emydine turtles 1 (outgroups removed for clarity). Nomenclature follows the respective references. *Top left:* Phylogeny based on morphological evidence (Gaffney & Meylan 1988). Synapomorphies: (1) plastral hinge and suprascapula present; (2) episcapula present. *Top right:* Phylogeny based on mitochondrial 16S rRNA sequences (redrawn from Bickham *et al.* 1996). *Bottom left:* Phylogeny based on mitochondrial 16S rRNA sequences plus morphological, ethological and life history evidence (redrawn from Burke *et al.* 1996). *Bottom right:* Phylogeny based on the mitochondrial cyt *b* and ND4 genes and adjacent DNA coding for tRNAs (modified from Feldman & Parham 2002; weakly resolved relationships of *'Emys' blandingii*, *'E.' marmorata*, and *E. orbicularis* shown as polytomy).

Later molecular studies using other mitochondrial genes and nuclear loci (Lenk *et al.* 1999; Feldman & Parham 2002; Spinks & Shaffer 2009; Wiens *et al.* 2010) corroborated the paraphyly of *Clemmys*. In the course of a phylogeographic study of *Emys orbicularis* based on cyt *b* sequences and using all other emydine genera as outgroups, Lenk *et al.* (1999) found a well-supported clade containing *Emys*, *Emydoidea* and *C. marmorata*, albeit with weakly resolved sister group relationships of these taxa. The same topology was confirmed by Feldman & Parham (2002), who used in addition to the cyt *b* gene sequence data of the ND4 gene and flanking DNA coding for tRNAs (Fig. 3: bottom right). Furthermore, the phylogenetic analyses of Feldman & Parham (2002) revealed, with weak support, *Clemmys guttata* as sister of *Terrapene*, and this clade constituted the sister group of (*C. marmorata*, *Emydoidea*, *Emys*); *C. insculpta* + *C. muhlenbergii* were, as the sister group of the two other more inclusive clades, the most basal group. This unexpected situation implied that the complicated morphological structures associated with the plastral hinge were either developed twice in the lineages of *Emys* + *Emydoidea* and *Terrapene*, or lost twice in *C. guttata* and *C. marmorata*.

Recognizing the paraphyly of *Clemmys*, two independent studies (Holman & Fritz 2001; Feldman & Parham 2002) suggested a revised classification to establish monophyletic genera. Holman & Fritz (2001) proposed to transfer *C. insculpta* and *C. muhlenbergii* to the resurrected genus *Glyptemys* Agassiz, 1857 and *C. marmorata* in the monotypic genus *Actinemys* Agassiz, 1857. In doing so, Holman & Fritz (2001) acknowledged the considerable morphological differences between *Actinemys*, *Emydoidea* and *Emys*, exceeding by far the extent of the morphological distinctiveness as occurring among species of many other chelonian genera (Figs 4–7; Table 1). This taxonomic scheme was later also endorsed by Ernst & Lovich (2009). In contrast, Feldman & Parham (2002) suggested lumping *C. marmorata* with *Emys orbicularis* and *Emydoidea blandingii* in an expanded genus *Emys*. One of their arguments, which was later repeated by others (Spinks & Shaffer 2009), was that with this arrangement not only a phylogenetically informative nomenclature were achieved, but also that the historical allocation of all three species in the genus *Emys* was reinstated. As outlined above, about 90 species representing 10 distinct families were included in *Emys* during the 19th century, not necessarily supporting the logic of this historical argument.

TABLE 1. Significant morphological characters of *Actinemys marmorata*, *Emys orbicularis*, *E. trinacris*, and *Emydoidea blandingii*.

	Actinemys	*Emys*	*Emydoidea*
Plastral hinge	–	+	+
Bridge	bony, solid	cartilaginous	cartilaginous
Entoplastron	roundish	diamond-shaped with long posterior spine	diamond-shaped with long posterior spine
Suprascapula	–	+	+
Episcapula	–	–	+
Skull	not elongated	not elongated	elongated
Triturating surfaces	broad	broad	narrow
Cervical vertebrae	not elongated	not elongated	strongly elongated
Free thoracic rib heads	small	small	large, strongly bent

Like Holman & Fritz (2001), Feldman & Parham (2002) placed *C. insculpta* and *C. muhlenbergii* in a distinct genus, but selected for it the name *Calemys* Agassiz, 1857. Since both *Calemys* (type species *Testudo muhlenbergii* Schoepff, 1801) and *Glyptemys* (type species *Testudo insculpta* LeConte, 1830) were simultaneously published in the same work (Agassiz 1857), the First Reviser Principle (ICZN 1999: Article 24) determined that the precedence of *Glyptemys* was fixed by the earlier published paper by Holman & Fritz (2001). As a consequence, *Glyptemys* became the valid name for the genus accommodating the species *G. insculpta* and *G. muhlenbergii*. The sister group relationship of these two species, and a basal position of *Glyptemys*, was confirmed by all subsequent studies and, therefore, is not discussed further below.

Using combined molecular and morphological data, Stephens & Wiens (2003) came to the same conclusions with respect to the paraphyly of *Clemmys*, and endorsed a nomenclatural arrangement corresponding to that of Holman & Fritz (2001), with *Actinemys* as a monotypic genus for the species *A. marmorata*, and with *Emydoidea* and

Emys as distinct genera. Stephens & Wiens (2003) acknowledged in their study the morphological distinctiveness of *Emydoidea* that achieved an amazing degree of convergent similarity to *Deirochelys*.

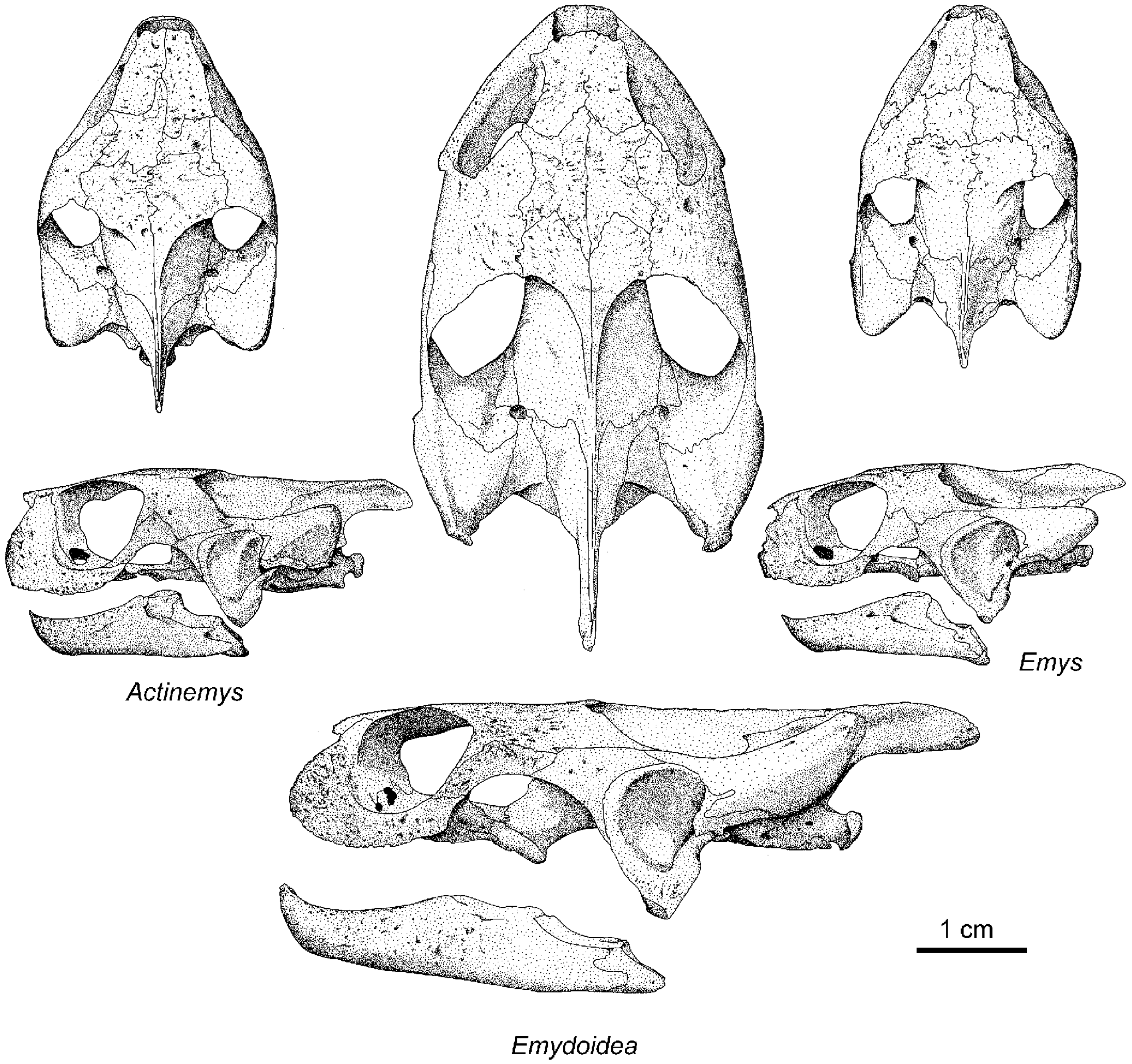

FIGURE 4. Dorsal and lateral views of skulls of *Actinemys marmorata* (Museum of Zoology Dresden, MTD 24914), *Emydoidea blandingii* (MTD 44419), and *Emys orbicularis* (MTD 44202). Note much elongated skull shape in *Emydoidea*. Drawings: C. Schmidt.

Spinks & Shaffer (2009) found strong disagreement between mitochondrial and nuclear gene trees for *Actinemys*, *Emydoidea*, and *Emys*, even though their monophyly was well-supported. Sequence data of the mitochondrial cyt *b* gene weakly supported a sister group relationship of the North American taxa *Actinemys* + *Emydoidea* (Fig. 8: top left), but three nuclear loci (non-coding introns: HNF-1α, RELN, R35) supported a sister group relationship of *Emydoidea* + *Emys* (Fig. 8: top right). These findings were interpreted as the result of an ancient hybridization event (12 million years ago), leading to mitochondrial introgression. In this study, nuclear data suggested *Clemmys guttata* as sister to a clade ((*Emydoidea* + *Emys*) + *Actinemys*) + *Terrapene*. In contrast, mitochondrial sequences favored with high support a sister group relationship of *Clemmys guttata* + *Terrapene,* and this clade constituted the sister group of (*Actinemys* + *Emydoidea*) + *Emys*. Spinks & Shaffer (2009) concluded that the recognition of three genera (*Actinemys* for *marmorata*, *Emydoidea* for *blandingii*, and *Emys* for *orbicularis* and *trinacris*) obscures, rather than illuminates, the phylogenetic relationships of these turtles, but did not comment on the contradictory situation with respect to *C. guttata*.

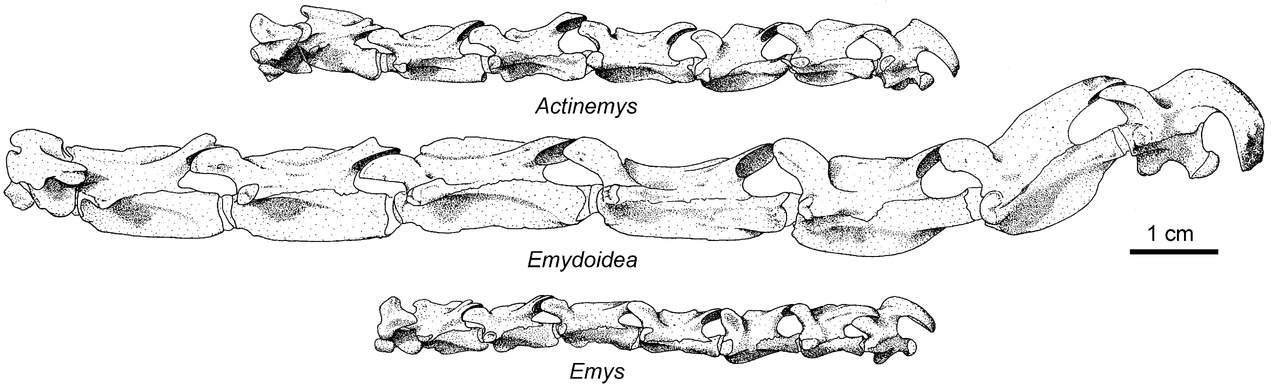

FIGURE 5. Neck vertebrae of *Actinemys marmorata* (Museum of Zoology Dresden, MTD 24915), *Emydoidea blandingii* (MTD 44419), and *Emys orbicularis* (MTD 44202). Note elongated vertebrae in *Emydoidea*. Drawings: C. Schmidt.

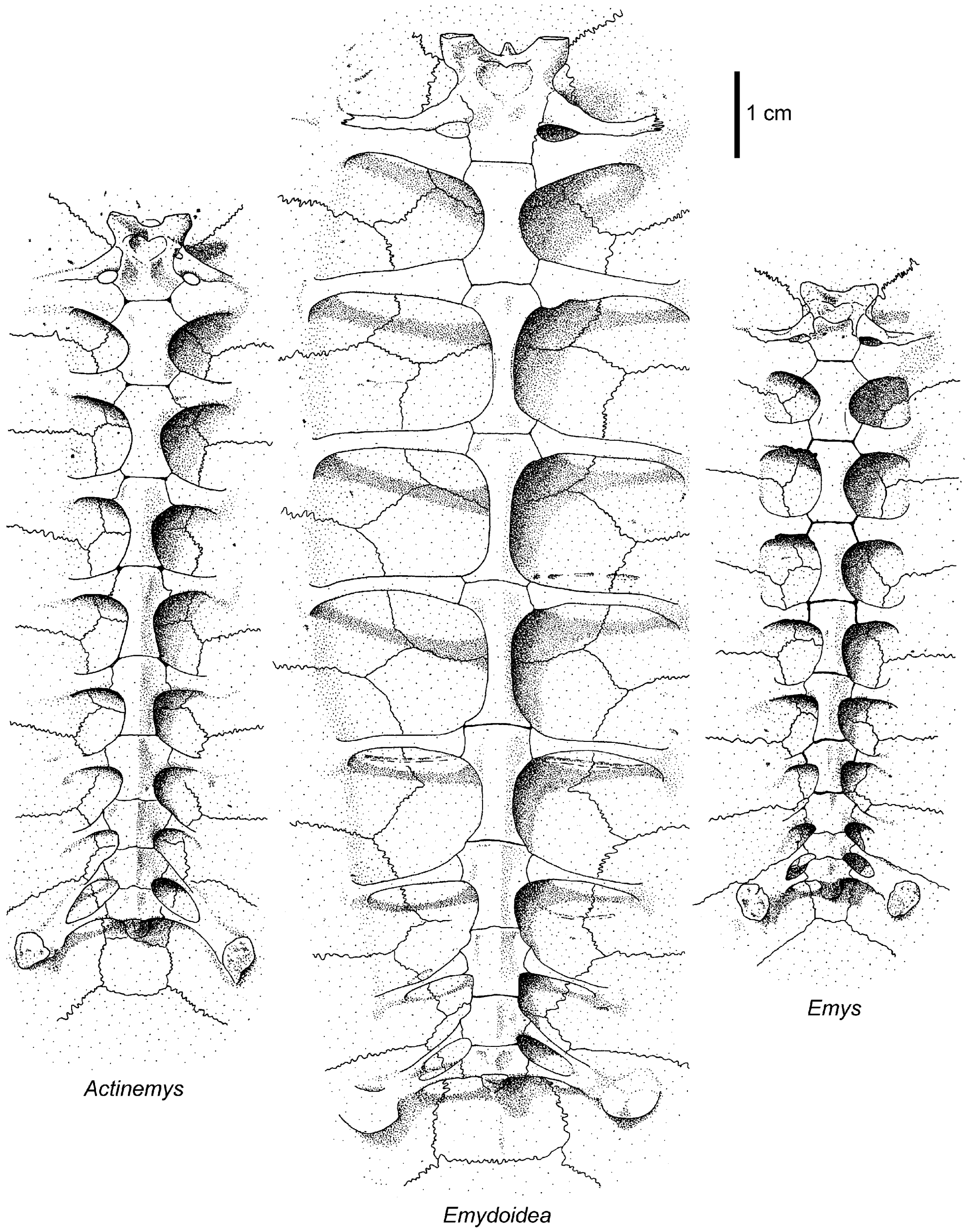

FIGURE 6. Thoracic ribs of *Actinemys marmorata* (Museum of Zoology Dresden, MTD 24914), *Emydoidea blandingii* (MTD 8480), and *Emys orbicularis* (MTD 44202). Note enlarged, strongly bent thoracic ribs in *Emydoidea* serving for anchorage of neck muscles. Drawings: C. Schmidt.

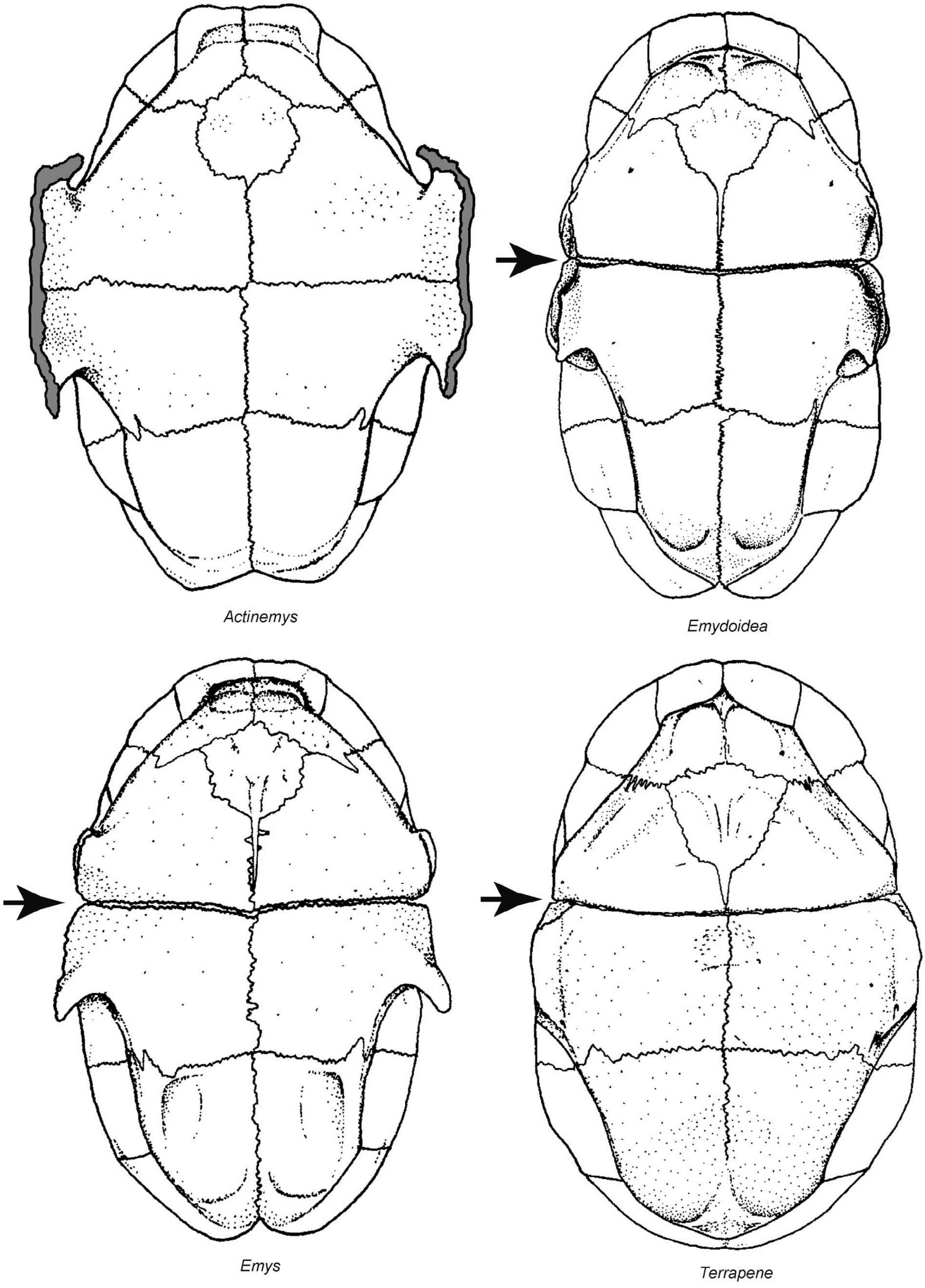

FIGURE 7. Visceral (dorsal) view of plastra *top from left to right: Actinemys marmorata* (Michigan State University Museum, MSU 14447), *Emydoidea blandingii* (Museum of Zoology Dresden, MTD 8480), and *bottom from left to right: Emys orbicularis* (MTD 12363), *Terrapene carolina* (MTD 8481). *Grey bridge region* in *Actinemys* indicates solid bone; in the other taxa, the bridge region of adult turtles is a ligamentous connection between carapace and plastron. *Arrows* in *Emydoidea*, *Emys* and *Terrapene* indicate plastral hinges. Note different shapes of entoplastra. Modified and reproduced from Holman & Fritz (2001).

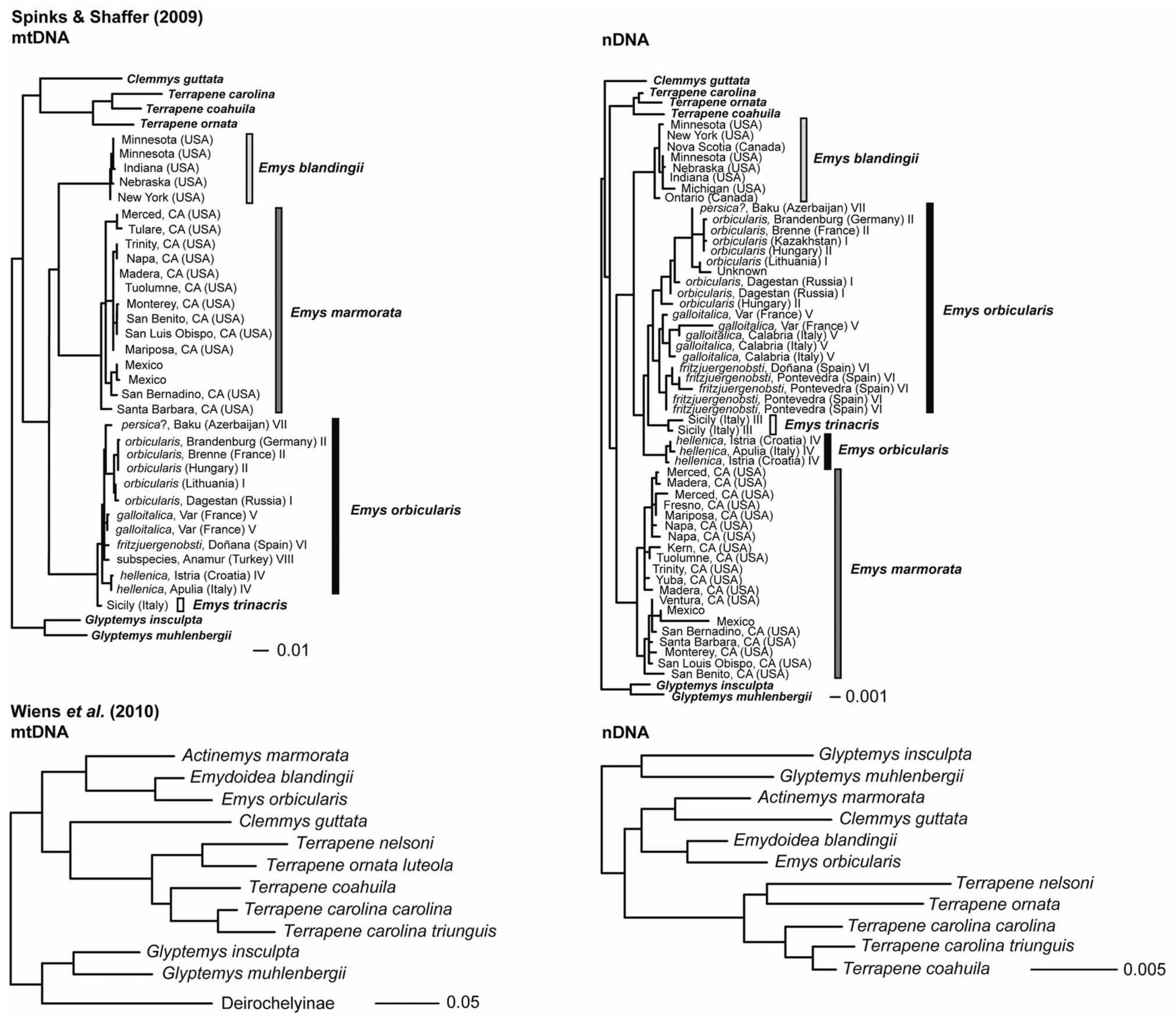

FIGURE 8. Phylogenetic hypotheses for emydine turtles 2 (outgroups removed for clarity). Nomenclature follows the respective references except for *Emys orbicularis* in the two upper trees. Here, the subspecies names and mitochondrial lineages according to Lenk *et al.* (1999), Fritz *et al.* (2005, 2007, 2009) and Pedall *et al.* (2011) are given. Branch lengths in the upper trees are Maximum Likelihood divergence estimates; bottom, Bayesian divergence estimates. *Top left:* Phylogeny based on the mitochondrial cyt *b* gene (redrawn from Spinks & Shaffer 2009). *Top right:* Phylogeny based on three nuclear loci (non-coding introns: HNF-1α, RELN, R35; redrawn from Spinks & Shaffer 2009). Note the short basal branch lengths of more inclusive clades. *Bottom left:* Phylogeny based on the mitochondrial cyt *b* and ND4 genes (redrawn from Wiens *et al.* 2010; the sister group relationship of *Glyptemys* and the Deirochelyinae is very weakly supported). *Bottom right:* Phylogeny based on six nuclear loci (coding: NGFB; introns: ETS, GAPD, ODC, R35, Vim). Redrawn from Wiens *et al.* (2010).

Another study by Wiens *et al.* (2010) using mitochondrial and nuclear DNA sequences yielded different results. Like Feldman & Parham (2002) and Spinks & Shaffer (2009), Wiens *et al.* (2010) found in their mitochondrial data set (cyt *b*, ND4) a sister group relationship of *C. guttata* and *Terrapene* spp., and this clade constituted the sister group to (*Emydoidea* + *Emys*) + *Actinemys* (Fig. 8: bottom left). However, using six nuclear loci (coding: NGFB; introns: ETS, GAPD, ODC, R35, Vim), Wiens *et al.* (2010) revealed a well-supported novel clade that included *C. guttata* as sister species of *Actinemys*, and this clade was the sister group of *Emydoidea* + *Emys* and *Terrapene* the successive sister of ((*Actinemys* + *C. guttata*) + (*Emydoidea* + *Emys*)) (Fig. 8: bottom right).

This situation suggests that the nuclear data sets of both author teams might be heavily impacted by lineage sorting problems and that the phylogenetic resolution is still insufficient. When it is considered that mtDNA represents one and the same locus and that it is inherited only in maternal line, this could also apply to the conflicts between mitochondrial and nuclear trees. We cite here Wiens *et al.* (2010): “Additional analyses, including more nuclear loci, may be necessary to resolve [the] relationships [of *Actinemys*]. Although Spinks & Shaffer (2009) argue that *Actinemys* and *Emydoidea* should be placed within *Emys*, there is no phylogenetic justification for this change, and it leads to unnecessary instability in the long-standing generic names *Emys* and *Emydoidea*. Most importantly, our analyses of the combined nucDNA data show *Emys* (sensu Spinks & Shaffer, 2009) to be non-monophyletic, given that *Actinemys* clusters with *Clemmys guttata* […] with very strong support."

Exodos

In conclusion, what remains well-supported among all phylogenetic hypotheses are three matters: (1) the paraphyly of the former genus *Clemmys* sensu lato, (2) the basal position of the former *Clemmys* species *insculpta* and *muhlenbergii* within the Emydinae, and (3) the monophyly of *Emydoidea blandingii* and *Emys orbicularis* + *Emys trinacris*. In contrast, the phylogenetic position of the former *Clemmys* species *guttata* and *marmorata* varies considerably among different phylogenetic scenarios (Figs 3 and 8), making the inclusion of *marmorata* in the same taxon as *Emydoidea* + *Emys* unacceptable under a phylogenetic classification framework (*cf*. Wiens *et al*. 2010).

Epilogos: Are monotypic genera desirable?

Much of the recent discussion on generic delineation of emydine turtles centered around the question of whether monotypic genera, i.e. comprising only a single species, should be recognized or not, and depending on the authors' personal positions the arguments put forward were either that such genera are not phylogenetically informative, and that *Emys* should therefore be expanded (Burke *et al.* 1996; Feldman & Parham 2002; Spinks & Shaffer 2009), or that the deep morphological gaps between *Actinemys*, *Emys*, and *Emydoidea* justify their recognition as distinct genera (Holman & Fritz 2001; Stephens & Wiens 2003). The insight that the phylogenetic position of *Actinemys* is by far less clear than thought before (Wiens *et al.* 2010) made much of the arguments for an expanded genus *Emys* obsolete.

In spite of what has just been said, we wish to explain that from a purely theoretical point of view the recognition of a monotypic genus is only unacceptable when it would cause the paraphyly of another genus. As long as this is not the case, it is only convention whether monotypic genera are desired or not. Our opinion is that, when there is a well-pronounced morphological gap separating a given species from the next monophyletic clade, only monotypic genera, or higher monotypic taxa, can indicate the extent of the morphological distinctiveness of the included unique species.

Chelonians include a fair number of monotypic genera and families (*cf*. Fritz & Havaš 2007; Rhodin *et al.* 2010). The taxonomic distinctness of most of these taxa has never been challenged, and appears unlikely to be challenged in the future. Prominent examples on the family and genus level are the Carettochelyidae, with the included monotypic genus *Carettochelys*, the Dermatemydidae, with the included monotypic genus *Dermatemys*, the Dermochelyidae, with the included monotypic genus *Dermochelys*, and the Platysternidae, with the included monotypic genus *Platysternon*. Examples among polytypic families are the monotypic genera *Macrochelys* (Cryptodira: Chelydridae), *Clemmys* sensu stricto, *Deirochelys* (Cryptodira: Emydidae), *Geoclemys*, *Hardella*, *Leucocephalon*, *Notochelys*, *Orlitia*, *Vijayachelys* (Cryptodira: Geoemydidae), *Claudius* (Cryptodira: Kinosternidae), *Chersina*, *Malacochersus* (Cryptodira: Testudinidae), *Amyda*, *Dogania*, *Palea*, *Trionyx* (Cryptodira: Trionychidae), *Chelus*, *Elusor*, *Platemys*, *Pseudemydura*, *Rheodytes* (Pleurodira: Chelidae), *Erymnochelys* and *Peltocephalus* (Pleurodira: Podocnemididae). Parenthetically it may be noted that one of the monotypic emydine genera, *Clemmys* sensu stricto, is also explicitly recognized by Feldman & Parham (2002) and Spinks & Shaffer (2009).

Furthermore, in the discussion on the generic classification of emydines it was often not sufficiently acknowledged that the monotypy of *Emys* sensu stricto and *Actinemys* is by far not axiomatic, rendering the debate also under this aspect obsolete. It has been suggested that *Actinemys* could be composed of more than one species (Holland 1994; Spinks & Shaffer 2005), and a second *Emys* species was described from Sicily, *E. trinacris* (Fritz *et al.* 2005). Population genetics confirmed the reproductive isolation of *E. trinacris*, and consequently its species status (Pedall *et al.* 2011), making one of the genera in question polytypic. Restricted gene flow between several genetic lineages within what is currently considered the polytypic species *E. orbicularis* (Pedall *et al.* 2011) resembles the situation of other Palaearctic herp taxa that are now regarded as complexes of distinct species (e.g., *Triturus cristatus* complex: Wallis & Arntzen 1989; Vörös & Arntzen 2010; *Bufo viridis* subgroup: Stöck *et al.* 2006; Colliard *et al.* 2010; *Hyla arborea* complex: Stöck *et al.* 2008; Gvoždík *et al.* 2010; *Lacerta viridis* complex: Rykena 1991; Böhme *et al.* 2007; Joger *et al.* 2007), so that it is likely that in future even more species of *Emys* will be recognized.

In any case, *Actinemys*, *Emydoidea* and *Emys* represent three morphologically highly distinct, old evolutionary lineages. The divergences among lineages within *Actinemys marmorata* (Spinks & Shaffer 2005; Spinks *et al.* 2009), between *Emys orbicularis* and *Emys trinacris*, and among lineages within *Emys orbicularis* (Lenk *et al.* 1999; Fritz *et al.* 2005, 2007, 2009) are distinctly younger than the basal split between *Actinemys*, *Emydoidea*, and *Emys* (3–4 million years ago *vs.* 12–17 million years ago; Lenk *et al.* 1999; Spinks & Shaffer 2009; Spinks *et al.* 2009; but see Wiens *et al.* 2010). Even when all of these three genera were monophyletic, lumping them in one and the same genus would mask that two lineages (*Actinemys*, *Emys*) include young radiations in western North America or the Western Palaearctic. When it is furthermore considered that the phylogenetic position of *Actinemys* is unclear (Wiens *et al.* 2010) and that the morphological distinctiveness of the three genera exceeds by far the divergence typically occurring among species of the same genus, a continued usage of the distinct genera *Actinemys*, *Emydoidea* and *Emys* seems advisable.

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