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Response to Arthur Georges' review of *Freshwater Turtles* of Australia (2017)

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In his review of the book *Freshwater Turtles of Australia* (hereafter *FTA*), Arthur Georges made the concluding comments that, while the book was a 'beautifully illustrated and spectacular expose of the diversity and form of the unusual turtle fauna of Australia' and 'an interesting read', it was not the reference book for researchers, academics and herpetologists as described by CSIRO Publishing, and that as a 'scientific resource for researchers, academics and herpetologists, . . . a poor example to follow'. Preceding this, Georges presents several criticisms, a major point of contention being his belief that one of the primary purposes of the book was to 'reshape the scientific classification of those turtles, through a taxonomic reevaluation', one he was disappointed with.

Georges is correct in that the primary purpose of the book was as an exposé of the Australian turtle fauna. The book was never intended as a major scientific resource; rather, it was meant to provide a platform to present the diversity of Australian turtles, and to provide direction for interested readers, by way of the numerous references cited, to further investigate their biology. There was no intention to 'reshape the scientific classification of . . . turtles' as suggested by Georges; rather, we were required to make decisions to arrive at a taxonomy we believe best reflected the diversity and form of Australian turtles and on a nomenclature that fell within the bounds of best practice. For some taxa this did not necessarily agree with the classification proposed by others.

We faced two issues in arriving at a suitable taxonomy. One was to evaluate incongruities in the level of discrimination provided by genetic and morphological data for some taxa. The other, the application of an appropriate nomenclature to the taxonomy, we chose to adopt. In his review, Georges criticises the taxonomic hierarchy we use, the way that taxonomy was presented and the nomenclature applied to that taxonomy.

A large part of Georges' review is spent highlighting cases of our apparent misinterpretation of genetic data in its application to the taxonomic decisions made in *FTA*. Neither of us (Cann or Sadlier) are skilled geneticists, and only used the information presented to us at its face value. Georges states we disagree with application of allozyme electrophoresis for delimiting species boundaries and that we denigrate good science in our assessment of his allozyme data. We have no issue with the quality of the allozyme studies as implied by Georges; rather, we have only questioned its limitations in identifying

biological entities (taxa) in some groups of turtles, where these show some degree of morphological differentiation but only limited genetic differentiation.

We provide a limited response (due to space limitations) to specific (bold) comments made in Georges' review, and encourage the reader to refer also to the text in *FTA* in judging whether we have erred to warrant the criticism levelled.

That 'Cann and Sadlier present a series of taxonomic rearrangement that reduce some species to the level of subspecies, use names that have been regarded by others as unavailable (Iverson *et al.* 2001), and elsewhere raise a plethora of geographic variants to subspecies'

On one occasion, Cann and Sadlier (2017) have reduced a species to the level of subspecies, for the Arnhem Land long-neck turtle *Chelodina* (*Macrochelodina*) oblonga burrungandjii. It is explicitly stated in *FTA* (pages 14–16) that the long-neck turtles from northern Australia have been the subject of a fluctuating taxonomy, and that the approach taken was to regard the morphologically and genetically distinctive regional forms as subspecies of *Chelodina* (*Macrochelodina*) oblonga. This approach was intended to highlight the extent of regional variation contained within this widespread taxon, that these regional groups (subspecies) represent emerging evolutionary units, incipient species, but with the associated issues of genetic introgression and morphological incongruence through hybridisation at contact zones as identified by Georges and Thomson (2010).

On two occasions, Cann and Sadlier (2017) have recognised taxa formerly regarded as subspecies as full species. In both instances, there was no supporting allozyme differentiation and the decision to recognise these taxa as species was made on the basis of morphological criteria (*Emydura worrelli* as a full species versus a subspecies of *subglobosa* and *Emydura krefftii* as a full species versus a subspecies of *Emydura macquarii*). The decision to do so was qualified with statements in *FTA* that in our opinion the level of differentiation provided by the allozyme data could have been too conservative to adequately reflect the differences between these taxa (*FTA*, page 16). This was not a case of 'morphology over molecules' as claimed by Georges; rather, we questioned the process of applying a single dataset (allozymes) to arrive at a taxonomy for some groups

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of turtles (primarily the species of *Emydura*). The comment regarding the potentially conservative nature of the allozyme data is not original, and not inconsistent with that made by one of Georges' own students in discussing the lack of differentiation between *Chelodina* (*Macrochelodina*) oblonga burrungandjii and *Chelodina* (*Macrochelodina*) oblonga walloyarrina for the allozyme loci and nuclear R35 intron that 'could be attributable to these techniques lacking the resolution to detect genetic differences' (Alacs 2008).

The raising of a 'plethora of geographic variants to subspecies' amounts to the recognition of the subspecies Chelodina (Macrochelodina) oblonga walloyarrina and of Chelodina (Macrochelodina) oblonga rugosa in the genus Chelodina (the reasons behind which are given above), and in the recognition of the subspecies of Emydura macquarii described by Cann in 1998. In FTA, the various subspecies of Emydura macquarii from eastern flowing drainages were recognised on the basis of differences in morphology that were regarded as evidence of evolutionary divergence between populations inhabiting different river systems, rather than as a phenotypic response to local conditions as interpreted by Georges and Thomson (2010). All but one of these subspecies described by Cann (1998) are cited as 'genetic clades' in an unpublished report by Georges et al. (2007), lending further support to these subspecies as representing geographically discrete evolutionary entities.

The statement by Georges that Cann and Sadlier (2017) 'use names that have been regarded by others as unavailable (Iverson et al. 2001)' presumably relates to the application in FTA of the names Elseya stirlingi to the species from the Johnstone Rivers of north-east Queensland and of the name Elseva jukesi to the species from The Alligator Rivers region of the Northern Territory. It is clearly stated in FTA that the use of these names was made in respect to the 'revisionary' work of Wells (2007a) which postdates Iverson et al. (2001), and validates the names for the taxa they were applied to. As such, as far as we are aware, these names are available and are the names that should be applied under the Code of Zoological Nomenclature. For the same reason, we use the name Wollumbinia proposed by Wells (2007b) for the saw-shelled turtles (formerly in Elseya) which predates the name Myuchelys created by Thomson and Georges (2009). This hardly amounts to a reshaping of the scientific classification of Australian freshwater turtles.

'They ignore ... Georges and Adams (1996) established a local benchmark for the Australian chelid turtles to assess differences consistent with variation among populations of a species, between closely related species, and between species in different genera'

A comment was made in FTA (page vi) regarding the use by Georges and Adams of fixed differences as the primary criteria used in defining species boundaries, specifically in the application of a '(minimum) number of fixed differences between suspected species in allopatry (three or more) or in sympatry (one fixed difference or substantial divergence without intermediates).' This statement was derived from the section on species delimitation in the article by Georges and

Adams (1996) which states 'Profiles of allozyme frequencies were determined for each population, and fixed differences between populations were tabulated ... Two populations were considered notionally to belong to different diagnosable taxa if all individuals in one population could be distinguished from all of the individuals in the other by one or more fixed differences', and 'as a rule of thumb . . . to cases of allopatry, we required at least two fixed differences when sample sizes were large . . . and at least three fixed differences when sample sizes were small ... to regard populations as separate diagnosable taxa'. Although not explicitly referred to as the 'local' benchmark (note - it does not appear as this in Georges and Adams 1996) the statement in FTA clearly identifies comments made by us on levels of fixed difference between species as coming from the publications by Georges and Adams and as taking into account what Georges and Adams (1996) regard as the 'rule of thumb'.

The book 'insufficiently assesses genetic evidence' with respect to 'the distinctiveness of *Chelodina kuchlingi* Cann, 1997'

We regard this criticism as presented out of context with respect to the main body of text in FTA. It is clearly stated that recognition of kuchlingi is in the light of information provided 'on the provenance of the type, the distinctiveness of the species carapace morphology, and the existence of other specimens attributable to this taxon on the basis of ... carapace morphology'. Reference to the cited genetic data is only as providing further support for the recognition of Chelodina (Macrochelodina) kuchlingi as a valid species.

The genetic information for which we have been criticised as deficient in assessing was explicitly attributed as coming from unpublished data provided by Bill McCord, a former collaborator and co-author with Georges on a publication (Georges *et al.* 1999) that addressed relationships of Australian side-necked turtles. It utilised several mitochondrial genes in its analyses (including CO1, the gene in question in this criticism). We found no reason to question the integrity of the unpublished genetic distance data provided by McCord.

A criticism of 'the analysis' with respect to 'the argument derived from the unpublished work of Erika Alacs'

This statement is in reference to our citing in FTA of genetic data from the thesis of Erika Alacs in the account of the Kimberley long-neck Chelodina (Macrochelodina) oblonga walloyarrina. The 'argument' appears as a single sentence (FTA, page 69) which states 'A comprehensive genetic study by Alacs (2008) which sampled long-neck turtles across northern Australia identified burrungandjii and walloyarrina as each belonging to separate and distantly related groups within the northern long-necks (using the mitochondrial ND4 gene), supporting the morphological distinction between the two taxa identified earlier by Thomson et al. (2000)'.

There was no 'analysis' of the data in the context as implied by Georges; rather, the single statement in *FTA* is consistent with the scheme of relationships apparent in the structure of the phylogeny for the mitochondrial ND4 gene as presented in chapter 6 of the thesis by Alacs. It is also consistent with

several statements made in the thesis, one of which (Alacs 2008: page 110) states 'In the mitochondrial gene tree, *Chelodina sp.* (Kimberley) formed a distinct haplotype lineage (Fig. 6.3) and supported the hypothesis proposed by Thomson *et al.* (2000) that based on diagnosable morphological characters the Kimberley form is a distinct taxon'. As such, the statement presented in *FTA* is consistent with the information contained within Alacs' thesis; that is, that the genetic data for the mitochondrial ND4 gene identifies *burrungandjii* and *walloyarrina* as belonging to separate and distantly related genetic groups within the northern long-necks – that is all that was said with regard to the genetic data from the thesis of Alacs for this taxon.

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As a part of this criticism, Georges presents the statement that the 'prospect of accompanying introgression of nuclear genes via the same route' clouds any interpretation that might be placed on morphological differences between the Arnhem Land and Kimberley populations of *C. burrungandjii*', an 'argument missed by the defence of the Kimberley populations as a separate taxon.' Yes, the point of 'introgression of nuclear genes via the same route' was missed. We could find no reference to such a statement regarding nuclear gene introgression in the thesis by Erica Alacs or in later publications dealing with these taxa (Georges and Thomson 2010; Ellis and Georges 2015) – perhaps our oversight lies in this argument post-dating the publication of *FTA*.

That 'Cann and Sadlier maintain that there was an endemic *Emydura* in the Bellinger River'

Following on from the criticisms of our treatment of genetic data, Georges presents an extensive case for the pitfalls of the application of the precautionary principle in its application to conservation actions with regard to the listing of the Emydura from the Bellinger River as a threatened population. This is an extended preamble by Georges to the statement that in FTA Cann and Sadlier maintain that there was 'an endemic Emydura in the Bellinger River, now lost through hybridisation and introgression with the introduced Emydura', but that no evidence was given to support this view. Two comments are made in FTA regarding the identity of the Bellinger River *Emydura*. One (page 267) states the 'population in the Bellinger River now appears to be dominated by the release of Emydura macquarii from other drainages that has swamped the original gene pool'; the other (page 266) that 'the identity of the population is now lost through interbreeding with other forms of *macquarii* released into the drainage', and is part of a caption relating to an image of a turtle from the Bellinger River photographed in 1990. The context of text accompanying these statements is in reference to the identity of the population ~1990 and whether it represented a native population. Neither comment made regarding the Bellinger River Emydura states or infers that we maintain there was once an endemic (diagnostically unique) taxon or population in the Bellinger River. In the event Georges has used 'endemic' in reference to a native (but not necessarily diagnostically unique) population, the question as to whether a population of *Emvdura* native to the Bellinger River once existed would appear to be open. While Georges et al. (2007) state 'the lack of a widespread unique haplotype would suggest that the Bellinger *Emydura* is not a natural endemic', they also concede that their data cannot provide a definitive answer as to whether the Bellinger *Emydura* is derived entirely from introductions or eliminate the possibility it may be derived from natural dispersal events from adjacent drainages (Georges *et al.* 2011).

Finally, with respect to the classification presented in FTA, Georges states it 'does not follow the lead given by Cogger et al. (1983) on some of the more contentious issues', the 'lead given by myself and Scott Thomson (2010), nor that of Turtles of the World compendium (Rhodin et al. 2017)', or with 'regard to the official list prepared by the Australian Society of Herpetologists (ASH 2016a)'. It is difficult to respond to the issue with regard to the reference to Cogger et al. (1983) as Georges does not specifically state the issue. That our classification does not follow the lead given by Georges and Thomson (2010) or that of the official list prepared by the Australian Society of Herpetologists (ASH 2016) is the same issue given Georges was the lead player in both cases, and the classification presented by the ASH in 2016 reflects that presented earlier by Georges and Thomson in their annotated checklist (2010). Other issues with this criticism lie in the chronology of some of the leads we do not follow. FTA was in proofs and/or in press at the time the ASH (2016) and Rhodin et al. (2017) lists were released, and as neither of us were members of ASH, we would not have been aware of the release of that list on the ASH website.

With regard to our not following the 'lead' provided by the official ASH list, we note that more than one year after this list was created there is still no indication of the acceptance of one of the more contentious names ratified in the ASH list by at least two government bodies (Queensland Department of Environment and Heritage Protection and Australian Government EPBC list of Threatened Species) in their threatened species listings. This relates to the proposal to use the generic name *Myuchelys* erected by Thomson and Georges in 2009 for the saw-shelled turtles in precedence over the earlier name *Wollumbinia* proposed by Wells in 2007 (Wells 2007b).

We do not at this point intend to debate the nomenclature we have adopted other than to say a decision was made to accept names available for taxa in accordance with the tenants of the International Code of Zoological Nomenclature, and we refer the reader to the article by Cogger *et al.* (2017) with regard to the validity of the stance behind the ASH classification. In the context of the rules underpinning the ICZN, the touted ASH list for turtles steered by Georges may ultimately be the one that contains illegitimate names, and thus is the one that has unnecessarily created a dual nomenclature. In concluding, we present a particularly appropriate statement from the discussion by Cogger *et al.* (2017) – 'The use of a particular taxonomic arrangement is not, and never can be, mandated by an individual or group, and always represents a hypothesis'.

Georges saw fit to finish his review of FTA with the statement that in his view 'it contains too many errors and misinterpretations to be a reference book' and 'would have benefitted greatly from some rigorous peer review'. We openly acknowledge our limitations and accept FTA will have errors and flaws – we've subsequently found errors in the book not presented by Georges that we consider of greater consequence.

We only counter that the substance of the criticisms presented in the Georges review raise their own concerns.

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