



Diversity of Australasian freshwater turtles, with an annotated synonymy and keys to species

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Abstract

There have been many substantial advances in our knowledge of Australasian freshwater turtle biodiversity in the last three decades, but the classification of genera and species is in dire need of review. The proliferation of names in unpublished manuscripts and in taxonomic works published in ephemeral (often privately printed) magazines, journals or books, without the benefits of peer review and often with little justification and scant diagnoses, many of which are not allowable nomenclatural actions under the International Code of Zoological Nomenclature, has led to considerable confusion. Taxonomy is punctuated by timely and rigorous revisions that bring a check on the proliferation of names for unsubstantiated taxa. This paper is not a comprehensive revision, but in it we provide an assessment of the current taxonomy of Australasian freshwater turtles, focusing on information available to establish the validity of taxa as biological entities (as opposed to the validity of the names). We include an annotated list of species, an outline of the taxonomic issues for those taxa that are controversial (leading in some cases to synonymies), keys to the identification of genera and species, and updated information on their distributions. We call upon the International Commission on Zoological Nomenclature to incorporate effective measures into the Code to prevent the destabilizing influence of the proliferation of names for taxa that have not been established as real biological entities through the normal processes of peer reviewed publication. The provision by the ICZN of a list of journals in which nomenclatural acts must appear in order to be valid, in addition to meeting the other provisions of the Code, is suggested as such a measure. Without such action, destabilization of our taxonomy will continue, the traditional Linnaean binominal nomenclature will be undermined, and credibility will build for other forms of nomenclature that are on a firmer scientific footing, but in other ways inferior.

Key words: Reptilia, Testudinata, Chelidae, Trionychidae, Carettochelyidae

Introduction

Australia is well known for its unique animal and plant diversity. Local radiation in isolation, coupled with the chance processes of genealogical coalescence, have generated a high level of endemism. If we exclude fish, Australia is among the leading nations in most measures of megadiversity and, with an estimated 755 reptile species, tops all countries in reptile diversity (Mittermeier et al., 1997). As the driest vegetated continent on earth, Australian freshwater turtles fare less well than on other continents, with species richness well behind that of Asia and North America. The Australasian turtle fauna is dominated by pleurodires (side-necked turtles) of the family Chelidae—found elsewhere only in South America and so of undisputed Gondwanan origin—with about 26 Australian species in 7 genera. To this we can add the distinctive *Carettochelys insculpta*, and 6 chelid and trionychid species from New Guinea, Roti and Timor to bring the tally to 32 species so far described (recent checklists by Fritz & Havaš, 2007; Turtle Taxonomy Working Group, 2007a; Rhodin et al., 2008b).

This species count for Australasia is by no means a consensus. In 1975, in his first edition of *Reptiles and Amphibians of Australia*, Harold Cogger (1975) observed that the taxonomy of Australian chelid turtles was in dire need of review. Despite many indications that such a review was pending (Legler, 1980; Legler & Cann, 1980; Legler, 1981; 1982; Cann & Legler, 1994; Thomson et al., 2000; 2006), and the injection of substantial molecular data (Georges & Adams, 1992; 1996; Georges et al., 1998; 2002), it has not materialised until now. The vacuum so created, frustrations with the slow pace of researchers bogged down in the exactitude of their science, and the new-found capacity for individuals to privately publish using innovations in computer and printing technology, have led to the proliferation of taxonomic names published in ephemeral (often privately printed) magazines, journals or books, without the benefits of peer review and often with little or no justification and scant diagnoses (e.g. Wells & Wellington, 1985; Cann, 1997a; McCord & Ouni, 2007b). More recent examples include the circulation, as pdf files on the internet, of species accounts in a series of documents of dubious standing, under the banner *Australian Biodiversity Record* (Wells, 2002a; b; 2007a; b; c; 2009), though they do not constitute publications under the International Code of Zoological Nomenclature (hereafter the Code) (ICZN, 1999; Fritz & Havaš, 2007). The focus for many authors appears to be on the process of assigning names, and not on undertaking the research and publishing the science necessary to bring new elements of biodiversity to light (Fritz & Havaš, 2007). As a result, understanding of the taxonomy and systematics of Australasian freshwater turtles is not advancing as a science as rapidly as it could be. Rather, collective understanding of the taxonomy of the turtle fauna has deteriorated since Cogger made his earlier observation, arguably to the point of confusion.

None of the issues outlined above are new, but the rate at which the unconventional accounts are appearing is accelerating and increasingly destabilizing. With the looming biodiversity crisis in which turtles appear to be central players (van Dijk et al., 2000), a stable nomenclature for taxonomic concepts that are part of the body of science could not be more important. Without it, resources can be diverted inappropriately (Georges et al., 2007), regulations that govern wildlife trade circumvented (Kuchling et al., 2007), biodiversity assessments distorted (Agapow et al., 2004; Isaac et al., 2004), and conservation effort wasted. The proliferation of scientific names, with little or no justification of the taxa to which they are applied, presents those who are outside taxonomy, but who rely upon a stable classification representative of actual biodiversity, with a confusing array of new names and name combinations. For example, there are six binominal name combinations available and in use for *Chelodina colliei*, a distinctive species whose biological identity is undisputed. The common name Oblong Turtle has far greater stability than the scientific binomen, an unfortunate consequence of this taxonomic destabilization (Pauly et al., 2009).

Taxonomy is punctuated by timely and rigorous revisions that bring a check on the proliferation of names for unsubstantiated taxa. This paper is not a comprehensive revision, but in it we provide a current assessment of the taxonomy of Australasian freshwater turtles, an annotated list of recognized species, an outline of the taxonomic issues for those taxa that are controversial (leading in some cases to synonymies), keys to the identification of recognized genera and species, and updated information on their distributions. Some of our decisions are likely to be contentious, but we have deliberately focused on making a clear distinction between the availability of a name (the purview of the International Code of Zoological Nomenclature) and the validity

of the taxon to which the name is applied, as a real biological entity (the purview of science). Evidence in support of a taxon as a real biological entity (e.g. a species or a clade) becomes part of the body of scientific knowledge through the established process of peer review. Hence in some cases, names that are available under the Code, but that apply to supposed taxa, unsupported by scientific evidence either in the original account or subsequently, are placed in synonymy. This is a necessary step because of the proliferation of names which, though available, are not accompanied by scientific evidence in support of the status of the taxon. We also call for action by the International Commission on Zoological Nomenclature to prevent or at least ameliorate the generation of available names divorced from the science necessary to demonstrate that they apply to real biological entities.

Taxon Delimitation

Concepts of species and higher taxa drive decisions on species delimitation and the definition of genera, and remain a controversial area for biology (Mayr, 1996; de Queiroz, 1998; Noor, 2002; Sites & Marshall, 2003; Sites, 2004; de Queiroz, 2005). Indeed, a universal species concept that has satisfactory utility in an operational sense has been elusive and may not be possible (Hey, 2001). Opinions and decisions on the species that comprise a fauna vary considerably depending upon the species concept applied. Given that a consensus on the concept of species is unlikely, it is important to clearly define what is meant by the term “species” in any taxonomic revision, to avoid miscommunication over the taxonomic entities under discussion. Our concepts of genera, species and taxa below the level of species follow. In particular, we recognize a number of taxonomic categories below the level of species, representing intraspecific genetic and morphological variation, and which may have strong geographic structure.

Terminal Lineages and Diagnosible Terminal Taxa

A lineage is a single line of direct ancestry and descent and is a term that can be applied to ancestral-descendant sequences of populations (de Queiroz, 1998). A terminal lineage is the most recent segment of a lineage leading to an extant population that is on an independent trajectory by virtue of geographic or reproductive barriers to gene flow. We view a *Diagnosable Terminal Taxon* as the aggregation of extant populations that are the descendants of a lineage which has diverged to the point of accumulating one or more diagnostic characters (all individuals can be assigned unambiguously). More strictly, a *Diagnosable Terminal Taxon* is the set of extant populations representing the most recently diverged lineage that can be distinguished from all other such lineages by one or more diagnostic characters, plus the clade comprising all of its descendent terminal lineages. In practice, a *Diagnosable Terminal Taxon* depends on the resolution of the techniques applied to detect diagnostic characters, in which case they are sometimes referred to as *Operational Taxonomic Units (OTUs)*. In the context of Australian freshwater turtle taxonomy, each discrete drainage system occupied by a widespread species is likely to contain a *Diagnosable Terminal Taxon* at some level of resolution. The phylogenetic species concept (*sensu* Cracraft 1983) has all *Diagnosable Terminal Taxa* as species, whether the distinction arose by accumulated change during and following reproductive isolation, or by accumulated change through geographic isolation alone. However as molecular and morphological techniques and analyses are refined, yielding ever increasing resolution, this approach could ultimately lead to the recognition of every turtle population in an isolated drainage as a species. This would lead to rampant and destructive taxonomic inflation (see also Isaac et al., 2004). We regard diagnosability as necessary but not sufficient to warrant recognition of a taxon at the level of species (Padial et al., 2009).

Evolutionarily Significant Units (ESUs)

Evolutionarily Significant Units are essentially monophyletic aggregations (clades) of what are regarded as ephemeral *Diagnosable Terminal Taxa*. The diagnosable taxa within an *ESU* are not considered to be significant in that they may not be on enduring independent evolutionary trajectories. They are regarded as ephemeral because no one of them in particular can be distinguished from the many that are destined for

extinction as the *ESU* evolves, or because no one of them can be distinguished from those others destined to be anastomosed through sexual reproduction and genetic exchange when they come into contact. Thus, an *ESU* is considered to be a cohesive unit which is itself on an independent evolutionary trajectory, but on a broader spatial and temporal scale than the many ephemeral diagnosable taxa that comprise it at any one point in time. *Evolutionarily Significant Units* are defined in various ways (Moritz, 1994; Vogler & DeSalle, 1994; Moritz, 1995; Barrowclough & Flesness, 1996; Crandall et al., 2000), with one widely accepted operational definition provided by Moritz (1994). Some authors, particularly those inclined to define species on the basis of divergent mitochondrial clades with well-defined spatial delimitation (often seeking morphological diagnosis *post hoc*), would regard distinctive *ESUs* as species without additional evidence or argument. We do not (see also Padial et al., 2009). Many of the suspected species of Australian freshwater turtle identified (but not necessarily named) by Cann (1998) and others are regarded in this paper as either *Diagnosable Terminal Taxa* (single drainages) or *ESUs*, but not species.

Species

Broadly, we adhere to the *Biological Species Concept* (*sensu* Mayr, 1969), which invokes reproductive incompatibility as the barrier to gene flow between species sufficient to maintain their identity. Species are essentially *ESUs* on evolutionary trajectories that are independent by virtue of reproductive isolation, not simply by virtue of current geographical circumstance. Biological species maintain their integrity as diagnosable entities in sympatry. Such species are considered to be real biological entities conceptually, but human constructs or hypotheses operationally, defined on examination of evidence of reproductive isolation where it exists, subjectively on magnitude of difference otherwise.

Subjectivity in the application of the *Biological Species Concept* arises from several sources. First, species arise through a process of speciation, in which the mechanisms of reproductive isolation evolve. As this process is ongoing, not all extant taxa (named or not) will have completed the process, and a subjective decision needs to be made as to whether the process has proceeded sufficiently for a taxon to be regarded as a species (Dobzhansky, 1941). Limited hybridization and introgression, not sufficient to obliterate the distinction between two taxa, needs to be admitted to any mature operational definition of species. In an example discussed later in this paper, *Chelodina rugosa* hybridizes in the wild with the phylogenetically distant *C. canni* (Georges et al., 2002; Alacs, 2008), presumably having come into contact relatively recently. Nevertheless, the two are regarded as species. In another example, taxa distinguished on characters that are not substantial (body size and associated attributes, colouration, ecological attributes) that have recently diverged *in situ*, and that freely interbreed in zones of contact might be regarded as a single biological species (as with *Emydura macquarii macquarii* and *E. m. emmotti*). Hybridization between species that is common in nature is also a consideration in decisions on whether or not such species are distinct enough to be placed in separate genera.

A second area of difficulty in applying the *Biological Species Concept* is in cases of allopatry. Island forms are particularly problematic, and so too are groups such as freshwater turtles, whose distributions often across a series of discrete geographic units (drainage basins). Under the *Biological Species Concept*, species are diagnosable entities that can include any number of *Diagnosable Terminal Taxa* and *ESUs*. The judgment on whether a diagnosable entity is sufficiently distinct in allopatry to be regarded as a biological species is difficult. For example, a chromosomal rearrangement can result in reproductive incompatibility among individuals and if it comes to fixation in a deme, can result in isolation of that deme from gene flow with other demes of the parent species (Coyne, 1994; Rieseberg, 2001). The chromosomal rearrangement creates a terminal lineage and subsequently, once divergence leads to the accumulation of detectable diagnostic characters, creates a *Diagnosable Terminal Taxon*. Reproductive isolation occurs and a biological species is established perhaps with cytogenetic diagnosability, but with minimal accompanying morphological or DNA sequence character divergence. Alternatively, two *Diagnosable Terminal Taxa* or two *ESUs* may have diverged substantially, beyond that normally observed in recognized biological species, yet may not have achieved reproductive isolation. In such cases, the end game of speciation (Dobzhansky, 1941), often played out as active character displacement in sympatry (Templeton, 1981), is not yet complete and the outcome not

yet determined (e.g. *C. rugosa* and *C. burrungandjii* in Arnhem Land, (Georges et al., 2002; Alacs, 2008). Species delimitation in allopatry is and has always been a matter of judgment, whether the data are morphological, molecular or behavioural (Richardson et al., 1986; Padial et al., 2009).

Georges and his colleagues (Georges & Adams, 1992; 1996; Georges et al., 2002) applied this judgment in a systematic way to the Australian chelid turtles using data from multiple nuclear markers scored using allozyme electrophoresis. They applied a series of stepwise paired comparisons between populations to establish a set of diagnosable taxa, and relied upon the relative conservatism of allozyme nuclear markers to argue that these diagnosable taxa could potentially be considered as biological species. Fixed allelic differences in sympatry (e.g. *Emydura victoriae* and *E. subglobosa worrelli*) or sufficient fixed differences in broad parapatry (e.g. *Myuchelys latisternum* and *M. bellii*) were regarded as sufficient indirect evidence of lack of gene flow when the opportunity existed, and hence evidence of reproductive isolation. Determinations for taxa in allopatry were made on the basis of a yardstick (e.g. *Elseya albagula* and *E. dentata*), comparing levels of divergence between presumptive species against those within and among well-accepted species. These species designations and the evidence presented in support of them has formed, in part, the basis for subsequent decisions on what species would be described and named using morphology and the basis, in part, for accepting the status of taxa as biological species in the annotated list included in this paper. Anchoring the divergence in allopatry sufficient for species designation to the level of divergence observed between related, well-established species is a pragmatic one, in the absence of direct evidence of reproductive incompatibility. It is a decision that must be made for allopatric forms when applying almost any species concept, though the criterion for distinguishing between species and diagnosable entities below that species varies (de Queiroz, 1998).

Finally, some authors adhere to the view that species should be monophyletic assemblages, as with higher taxa, and that the cladistic method has relevance for delineation of species. Phylogenetic methods are applied to *Diagnosable Terminal Taxa* and species are delineated as monophyletic assemblages of these terminal taxa. The depth at which the clades are chosen as species is subjective, preferably made on the basis of explicit criteria. This concept is incompatible with the *Biological Species Concept (BSC)*, because a population that diverges to the point of reproductive incompatibility will commonly leave populations of the parent species that are not reproductively incompatible yet that are paraphyletic with respect to the divergent population. These residual paraphyletic populations are a single biological species under the BSC, perhaps not even operationally diagnosable, and there is no requirement under the biological species concept to split them. Thus, a biological species can comprise the extant representatives of a diagnosable lineage and some but not all of its descendant clades, and so need not be a clade itself. In our view, phylogenetic analysis therefore has little to offer decisions on species delineation, regardless of the value of phylogenetic analysis in determining the relationships among species, or among *Diagnosable Terminal Taxa*, *ESUs* or other discrete diagnosable subunits within species. Although good phylogenies are available (Georges & Adams, 1992; Georges et al., 1998; Megirian & Murray, 1999), phylogenetic analyses have not been applied in assessing species status in the present paper.

Subspecies

The concept of subspecies is contentious, in part because variation below the level of species defies easy organization. Mayr (1963) defines subspecies as aggregates of local populations of a species inhabiting a geographic subdivision of the species' range, and distinguished taxonomically from other populations of the species. Subspecies are usually defined on the basis of some overt character(s) shared by most (or 75%, Amadon, 1949) of the individuals at what are usually a contiguous series of geographic locations (Patten & Unitt, 2002). A subspecies under this definition is not an evolutionary unit, but simply a "handle of convenience" (Mayr, 1882:594), a classification of populations within species that has some utility for the museum curator in organizing a collection, or perhaps for lawmakers who may see advantage in referring specifically to subsets of a species in conservation legislation or regulations. Such subspecies are named under the Code because of the convenience that accompanies doing so. They are not necessarily diagnosable and there is no necessary requirement that they be clades (monophyletic). Indeed, they can be defined on a

single overt character or on colouration that has well-defined geographical province, but which does not reflect underlying evolutionary relationships among populations (Burbrink et al., 2000).

When the subspecies name is applied to populations that are geographically isolated from other populations of the species, it is tempting to regard subspecies also as evolutionary units. Under this interpretation, subspecies are incipient species (Mayr, 1942), that is, geographically isolated populations that have diverged to the point of diagnosability, and so can be considered on independent evolutionary trajectories which, if continued, would ultimately lead to speciation. This interpretation of subspecies has been overtaken by more recent concepts of Evolutionarily Significant Units and Management Units (Moritz, 1994; 1995) for which there is no necessary imperative to assign a name.

In this paper, subspecies names are synonymised only where their concepts overlap or conflict at the taxonomic level of subspecies, and we make no particular judgements on their validity as biological entities, preferring to focus on the ranks of genus, subgenus and species. We follow Monroe (1982) and choose to use subspecies names (1) for allopatric populations where definition of the populations is clear, distinct, and total (or very nearly so—Amadon, 1949); (2) in situations where secondary contact between distinct populations has occurred and the zone of introgradation is relatively narrow; and (3) when the names are in use elsewhere in the scientific literature and have some utility. Subspecies that are not aggregates of populations (*sensu* Mayr, 1963) and that are defined for populations occupying single drainages (e.g. *Emydura macquarii gunabarra*, Hunter River, NSW, Cann, 1998) or occupying single islands with little or no internal geographic variation (Kuchling et al., 2007), are considered to add little value to understanding the evolutionary dynamics of species or to communication. They are not used, but nor are they synonymised for this reason alone, leaving the matter to be resolved through usage.

Hybrid species

Hybrids can have attributes drawn from both parent species, and so be intermediate, or can produce novel morphological attributes (e.g. the enlarged morphotype of hybrids between *Chelodina longicollis* and *C. canni*). Either way, they can be misidentified as independent entities and subsequently described as species (reviewed by Fritz & Havaš, 2007), some of which may have captive origins (Parham et al., 2001; Wink et al., 2001; Spinks et al., 2004; Stuart & Parham, 2007). Distinctive natural hybrids in the Australasian fauna variously regarded as species include "*Chelodina-novaeguineae longicollis* sp." (= *Chelodina canni* x *C. longicollis*, Cann, 1998:98)¹ and "*Chelodina* sp. *gulf*" (Cann, 1998:96) (= *C. rugosa* x *C. canni*) (Georges et al., 2002). While hybridization can be a positive force in speciation (Arnold, 1997; Mallet, 2005), no evidence has yet been presented to support any Australasian species as having a hybrid origin. Instances of natural hybridization with or without introgression are not regarded as sufficient evidence to diagnose and name any species with hybrid origins.

Genera

Unlike species, genera are human constructs both conceptually and operationally. They are useful in that they convey information—information on similarities of the species assigned to them, and information on their common collective differences from species of other genera. (Clayton, 1983) They are objective in the sense that they are required to contain only monophyletic assemblages of species (paraphyletic genera require remediation), but subjective in the sense that they carry more information on phenetic difference and similarity (shared primitive characters, and perhaps even morphological novelty, are often given greater weight) than conveyed solely by phylogeny.

Paraphyly of genera is resolved by either merging existing genera (lumping) or partitioning internal clades into separate genera (splitting). An example dealt with in this report is the paraphyly of the former genus *Elseya* *sensu lato* (including what is now *Myuchelys latisternum*). It could be resolved by treating *Elseya* as a junior synonym of *Emydura* (Gaffney, 1979; Frair, 1980; McDowell, 1983) or alternatively by splitting *Elseya* into those forms with affinities to *E. dentata* and those with affinities to *E. latisternum* (now *Myuchelys*

1. "... represent an intergrade population to the extent that species level has occurred" (Cann, 1998).

latisternum) into separate generic groups (Legler & Cann, 1980; Legler, 1981; Georges & Adams, 1992; Georges et al., 1998; Thomson & Georges, 2009). Splitting tends to create monotypic genera, which are undesirable as cladistic entities (not defined by shared derived characters) and because the information they convey in addition to that conveyed by the species designation is minimal—in marine turtles the genus designation is almost redundant. Every taxonomist takes what they regard to be a balanced view to these options even though those views may differ radically from those of their contemporaries (Turtle Taxonomy Working Group, 2007b). Our view is expressed in the treatment of the suggested genera below.

Limitations of molecular evidence

Molecular genetic techniques have proven of considerable value to systematics and taxonomy of turtles by bringing in new independent datasets and complementing traditional morphological approaches (McGaugh et al., 2007). DNA technologies have been particularly valuable in establishing phylogenies, but have been less effective in species delimitation (Sites & Marshall, 2003). In fact, allozyme electrophoresis, using proteins encoded by multiple independent nuclear genes to screen large numbers of individuals to detect fixed allelic differences, has yet to find an effective replacement in DNA sequencing technologies. Microsatellites are highly variable length polymorphisms useful for studies of population genetics (Goldstein & Schlötterer, 1999). However, because they are constrained in length, the probability of non-homologous alleles being of the same size and scored as identical increases unacceptably beyond closely related populations, even within a single species (Jarne & Lagode, 1996). This renders them of limited value for species delimitation. Single Nucleotide Polymorphisms (SNPs), nuclear introns, Amplified Fragment Length Polymorphisms (AFLPs, Vos et al., 1995) and Intersimple Sequence Repeats (ISSRs, Wolfe et al., 1998) are promising to provide a means for screening large numbers of individuals in search of fixed allelic differences useful for species delimitation (Martinez-Ortega et al., 2004; Gaines et al., 2005; Schmidt-Lebuhn, 2007; Shaffer & Thomson, 2007), but these multilocus techniques have been little used in chelonian studies (but see Fritz et al., 2005a; 2005b; 2007; Fritz et al., 2008) and so have yet to be fully capitalized as an alternative to allozyme electrophoresis.

Mitochondrial DNA markers (mtDNA), no matter how many are selected, are taken from a single maternally inherited unit. It is haploid, monomorphic in individuals (except rarely), and typically not subject to recombination (Rokas et al., 2003). Hybridization and introgression, both indications of lack of reproductive incompatibility, cannot be demonstrated using mtDNA data alone. Mitochondrial variation is lost relatively rapidly through drift because, as a maternally inherited haplotype genome, effective population size is a quarter that of nuclear markers. Typically for Australasian freshwater turtle species, there are only one or two major mitochondrial haplotypes, with minor variants, in each drainage system, so a fixed mtDNA difference is not the conservative tool it is in allozyme studies. Divergence between those uniquely retained haplotypes may reflect differential retention of ancient haplotypes rather than the time since separation of the populations that carry them, and hence be misleading, which is a particular risk for what is essentially a single character. For these and other reasons, mtDNA (or for that matter, any single feature) does not necessarily provide as reliable an indicator of species boundaries as a broader sampling of multiple independent nuclear genes or multiple morphological characters (Brower, 2006). Using divergent mitochondrial clades diagnostic for a well-defined geographical provenance to delineate species should be resisted, without adequate geographic sampling and without additional multi-character corroborative evidence drawn from the nuclear genome or morphology. Distinctive mitochondrial clades with well-defined geographical provenance exist in *Chelodina rugosa* (Alacs, 2008), *C. expansa*, *C. longicollis* (Hodges, unpublished data) and *Emydura macquarii* (Shaffer and Georges, unpubl. data), but each of these clades are not accorded status at the specific or subspecific level (but see subspecies designations for *E. macquarii*).

Nomenclatural Issues

Major reorganizations of the Australasian turtle taxa have been undertaken (Wermuth & Mertens, 1961; Goode, 1967; Cogger et al., 1983; Cann, 1998) and they have been included, with decisions on their taxonomy, in a number of recent global checklists (Fritz & Havaš, 2007; Turtle Taxonomy Working Group, 2007a; Rhodin et al., 2008b). The work by Cogger et al. (1983), in particular, was a well-considered foundation from which to draw a line and move forward in clarifying the taxonomy of Australian reptiles generally. There are also several guides for the identification of Australasian turtle species (Cann, 1998; Cogger, 2000; Iskandar, 2000; Auliya, 2007; Cann, 2008; Wilson & Swan, 2008).

The Wells and Wellington documents

Wells and Wellington (1983; 1985) created a host of destabilizing nomenclatorial novelties in their now infamous catalogues of Australian reptiles. Their action was severely criticized by the International Commission on Zoological Nomenclature (1991), the organization that regulates the use of scientific binomials in zoological taxonomy (through the Code), but to little effect.

New genera and species of Australasian turtle are now routinely introduced in hobbyist magazines (Cann, 1997a; b; c; d; McCord et al., 2003; McCord et al., 2007a; McCord & Ouni, 2007a; b) and privately published works (Cann, 1998), all allowable under the Code, and additional genus and species names have also been introduced in pdf files circulated on the internet (Wells, 2007a; b; c; 2009). While some accounts are of undoubted value (e.g. Cann, 1998), many present scant diagnosis and there is little or no application of science to demonstrate that the taxon is valid (as opposed to the name) or that it is assigned at the appropriate taxonomic level. Many accounts contain misleading or incorrect information (though this has no bearing on the validity of the name). Gross errors of nomenclature abound (see Iverson et al., 2001; Thomson, 2006). Scientific peer review, in the sense of putting one's work before the most rigorous scientific scrutiny available, is bypassed.

Iverson et al. (2001) assessed the validity of the turtle names of Wells and Wellington (1985) under the Code that operated at the time of publication. We have used these names where there is corroborating evidence, published in the primary literature, that the species is a valid taxon. The more recent attempts at nomenclatorial action by Wells (2007a; 2007b; 2007c; 2009) are not considered publications for the purposes of nomenclature as they violate ICZN Articles 8 and 9 and Recommendation 8D (see also Fritz & Havaš, 2007). The names that appeared in the documents (Wells, 2007a; b; c; 2009) are not considered available and are not used.

The descriptions by Wells and Wellington (1985) epitomize the worst of bad science. They purport to describe new species, but often include little or no description, diagnoses are scant and often patently erroneous, the reader is referred to pictures and illustrations elsewhere in the literature and expected to draw their own conclusions without guidance, and there is no analysis of characters or evidence of consistency of diagnostic characters across individuals of the taxon (Table 1). Specimens examined are not listed, and many key specimens in species descriptions may well not have been examined by the authors. Scientific peer review, an essential ingredient in the passage of new knowledge into the body of science, is not undertaken. The names for some of their taxa may be valid under the Code, but the science supporting the taxa as biological entities is almost entirely lacking.

The new generation of taxonomists has not only to contend with the imposing weight of deconstructing often inadequate 18th and 19th century descriptions, dealing with complex synonymies and locating scattered type material (Godfray, 2002), but they must contend also with the modern proliferation of equally inadequate species descriptions and other unnecessary and destabilizing nomenclatorial changes of the type generated by Wells and Wellington (Wells & Wellington, 1983; 1985; Wells, 2007a; b; c; 2009) and others. Taxonomists are distracted from the main game of serving the broader community with stable and informative classifications and bringing new biodiversity to light. Funding agencies might be forgiven for seeing alpha taxonomy as poor value for money.

Table 1. One of the descriptions of Wells and Wellington (1985) that survives scrutiny of its nomenclatural validity under the International Code of Zoological Nomenclature (Iverson et al., 2001). The name may be valid, but there is little or no evidence presented for the validity of the taxon to which the name is applied. The diagnostic feature is demonstrably false, as many populations of *Myuchelys latisternum* (formerly *Elseya latisternum*), including those from where the holotype is drawn, have a bright yellow facial streak.

Elseya purvisi

Holotype: Australian Museum R44654. Mature female collected in a river 15km S., 32.3km E. of Nowendoc, New South Wales (31 39'S X 152 04'E, elevation 183m) by J. Legler et. al., on 23 February, 1973.

Diagnosis: A member of the *Elseya latisternum* complex readily separated from all other *Elseya*, by the excellent illustrations and descriptions of Cann (1978: Plate 65, mature male, Plates 66-67, mature female, Plate 64 habitat of this species). The presence of a bright yellow facial streak readily separates this species from *Elseya latisternum*. Found in rivers of north-eastern New South Wales. Cogger (1983) provides diagnostic illustrations of its nearest relative, *Elseya latisternum* (Plates 408–410). Etymology: Named for Malcolm Purvis of North Sydney, New South Wales, noted herpetologist.

The role of the ICZN has been immensely important in contributing to nomenclatural consistency and stability. However, the ICZN sees its role as providing the regulatory framework for nomenclature (Tubbs, 1992), and that decisions on the validity of taxa as biological entities, as opposed to the availability of names for those taxa, is a matter for the scientific community. It took no further action on the Wells and Wellington document (1985), and remains deeply resistant to addressing the problem in an effective way, such as maintaining a list of refereed journals (print or online) in which species descriptions must appear. Proposals to revise the Code (ICZN, 2008) to meet some of the concerns outlined in this paper are overly complicated, and easily circumvented by those committed to the word but not the spirit of the Code. The broader taxonomic community is largely unaffected by events in reptile taxonomy, diminishing any collective will to take action. Leaving the decisions on the validity of the Wells and Wellington taxa (as opposed to the names) to the scientific community assumes some level of collective organization by that community. There is no body equivalent to the ICZN for assessing the validity of taxa. This is left for the process of scientific peer review. When scientific peer review is circumvented, as it is in the plethora of recent nomenclatural acts in hobbyist magazines, privately published works, and pdf files circulated on the internet (some potentially meeting the requirements of the Code, *albeit* minimally), there is no mechanism for an effective collective response from the scientific community. The ICZN needs to take urgent action to empower the scientific community to restrict names to those entities for which a case has been made, in the peer reviewed literature, for their validity as biological taxa. We need a positive list of journals in which nomenclatural acts must appear in order to be valid, in addition to meeting the other provisions of the Code. The imperative is all the greater as we move into the electronic age. Otherwise, we can expect a continuation of destabilization of our taxonomy, undermining of the traditional Linnaean binominal nomenclature, and increasing credibility for other forms of nomenclature that are on a firmer scientific footing (e.g. the PhyloCode, Joyce et al., 2004; Cantino & de Queiroz 2007) but also destabilizing.

List of Acronyms and Conventions

AMS	Australian Museum, Sydney, Australia.
AMNH	American Museum of Natural History, New York, USA.
BMNH	British Museum (Natural History), London, UK.
ICZN	International Commission on Zoological Nomenclature.
MCG	Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy.
MCZ	Museum of Comparative Zoology, Cambridge, USA.
MTD	Museum für Tierkunde, Dresden, Germany.
MNHP	Muséum National d'Histoire Naturelle, Paris, France.
NHMW	Naturhistorisches Museum, Wien, Austria.
NTM	Museum and Art Galleries of the Northern Territory, Darwin, Australia.
OUM	Natural History Museum of the Oxford University, Oxford, UK.
QM	Queensland Museum, Brisbane, Australia.
WAM	Western Australian Museum, Perth, Australia.
ZMB	Museum für Naturkunde, Humbolt-Universität, Berlin, Germany.

The conventions on the availability of names laid down in the International Code for Zoological Nomenclature (ICZN, 1999) are followed. Synonymies and references to the first usage of name combinations appear under the names of taxa we consider to be valid. The sequence of nominal taxa (suborder, family, genus, species, subspecies) is in alphabetical order, except in the case of subspecies in which the nominotypical subspecies is listed first. Type species of genus-group names are given as the combination used in the original account. Where the type species is uncertain, one is designated. Original species-group names are given in the species-group accounts. Authors are attributed to new species by normal conventions; new name combinations are separated from their authors by a dash. Distributional data are original and can be obtained from <http://iae.canberra.edu.au/cgi-bin/locations.cgi> The keys apply to adults of the species and subspecies, there being insufficient information on juveniles. In a few instances, where reliable external diagnostic characters are not available, the distinction is made on geographic locality.

Australasian Freshwater Turtles

The Australasian freshwater turtle fauna is drawn from the Families Chelidae (32 species), found elsewhere only in South America; Trionychidae (2 species), widespread in Asia, Africa, the Indo-Australian archipelago and North America; and the monotypic Carettochelyidae restricted to southern New Guinea and northern Australia.

Order Testudines Batsch, 1788

Key to Suborders and Families

- 1 Forelimbs paddle-shaped, without distinct ankle-joints or distinct clawed feet, or if not, with three or fewer claws on each foot. Pelvis not fused to plastron. Head and neck withdrawn straight back into the shellsuborder **Cryptodira** 2
- Forelimbs with distinct ankle-joints and distinct clawed feet, not paddle-shaped, with four or more claws on each foot. Pelvis fused to plastron. Head and neck withdrawn sideways into the shell...suborder **Pleurodira**.....**Chelidae**
- 2 Nostrils at the end of a tubular, fleshy snout or proboscis..... 3
- Nostrils level with the surface of the snout, no fleshy proboscis; marine 4
- 3 Forelimbs with two claws; margin of carapace rigid..... **Carettochelyidae**
- Forelimbs with three claws; margin of carapace flexible **Trionychidae**
- 4 Limbs with claws **Cheloniidae**²
- Limbs without claws **Dermochelyidae**²

Suborder Cryptodira Cope, 1868

Family Carettochelyidae Boulenger, 1887

Genus *Carettochelys* Ramsay, 1886 (Two-Clawed Turtles)

1886 *Carettochelys inculptus* Ramsay, 1886, [= *Carettochelys inculpta*], type species by monotypy.

Cryptodirous (neck withdrawn straight back into shell); no epidermal scutes overlying the shell, covered instead with continuous skin; bony plates of carapace, plastron and skull with small, round rugosities and wavy irregular raised lines between shallow sculptures (often not evident in live animals); carapace deep with a median keel toward the rear; peripheral bones complete and well developed, margin of shell rigid; plastron, small, forming a continuous plate without fontanelles, moderately flexible; forelimbs paddle-shaped, first two digits clawed, remaining digits strongly webbed; hindlegs also with two claws, but shorter; jaws with horny sheaths; nostrils at the end of a fleshy, truncated, pig-like snout; dorsal surface of tail with a series of crescent-shaped scales.

Carettochelys inculpta Ramsay, 1886 (Pig-nosed Turtle)

1886 *Carettochelys inculptus* Ramsay, 1886, Holotype, AMS R3677, from Fly River, [Papua] New Guinea.

1889 *Carettochelys inculpta*—Boulenger, 1889.

2003 *Carettochelys canni*—Artner, 2003

Detailed descriptions of morphology provided by Ramsay (1886), Waite (1905) and Walther (1922), summarized by Pritchard (1979) and Georges et al. (2008). Distinctive, species status beyond doubt. No subspecies are recognized³, and no published data exist to establish differentiation of New Guinea and Australian populations.

Family Trionychidae Bell, 1828a (Three-clawed Plateless Turtles)

Cryptodirous; no epidermal scutes overlying the shell, covered instead with continuous skin; carapace shallow with flattened flexible margins; peripheral bones absent (except in *Lissemys*); plastron reduced, with lateral and median fontanelles, flexible; first three digits of forelimbs clawed, remaining digits strongly webbed; hindlegs also with three claws, but shorter; jaws concealed under fleshy lips; nostrils at the end of a fleshy, elongate, tubular snout. A family with approximately 30 living species in North America, Africa, Asia, and New Guinea.

Genus *Pelochelys* Gray, 1864b (Giant Softshelled Turtles)

1864 *Pelochelys cantorii* Gray, 1864b, type species by subsequent designation (Günther, 1865).

A genus of very large soft-shelled turtles found in India, South-east Asia, the Philippines and New Guinea. Broad head, orbits well forward; lacks femoral flaps used to conceal the hind limbs; post-orbital arch slightly broader than the orbit.

Key to Australasian Species

- 1 Dorsal surface overlying the bony shell with distinct but irregular radiating pattern of yellow-brown stripes on a dark brown background; stripes extend along the dorsal surface of the neck toward the head; flexible margins of carapace with a marbled pattern of reticulations and spots; juveniles with rough-textured, tuberculate, patternless, brownish carapace; New Guinea, south of the central dividing range ***bibroni***
- Dorsal surface of shell and neck a uniform colour; juvenile carapace smooth, except for low tubercles in the nuchal region and longitudinal ridges in central bony disc area, with a distinct dark pattern of close-set dots; New Guinea, north of the central dividing range..... ***signifera***

2. Not considered further in this document.

3. Wells (2002a) separated the Australian populations of *Carettochelys inculpta* from those of New Guinea as subspecies, and assigned them names, but the account appears in a document that does not, in the opinion of the authors, meet the provisions of ICZN Articles 8 and 9 and Recommendation 8D and so is not considered a publication for the purposes of nomenclature.

Pelochelys bibroni (Owen, 1853) (New Guinea Giant Softshell Turtle)

1853 *Trionyx (Gymnopus) bibroni* Owen, 1853, neotype (Webb, 1995), AMS 3425, 3426, 131315 [single specimen, in parts], from Laloki River, Astrolabe Range, 40 miles from its entry into Redscar Bay (9°20'S, 147°14'E), Central District, Papua New Guinea.

1864 *Pelochelys bibronii* [sic]—(Gray, 1864b). First use of combination.

Redescribed and restricted to the southern lowlands of New Guinea by Webb (1995). Genetic divergence from *P. cantorii* confirmed by Engstrom et al. (2004), but yet to be compared genetically with *P. signifera*. No geographic variation has been reported within the species' restricted range and no subspecies have been named.

Distribution: Southern New Guinea from Setakwa River in West Papua to the Brown-Laloki River system in Papua New Guinea. Anecdotal reports of breeding on Sabai Island, Australia.

Pelochelys signifera Webb, 2002 [2003] (Variegated Giant Softshell Turtle)

2003 *Pelochelys signifera* Webb, 2002 [2003], holotype, BMNH 1921.11.11.4, from Wanggar River, Weyland Range, Geelvinck Bay, N. New Guinea (Papua Province, Indonesia)

Described largely on characteristics of a juvenile specimen, coloration and texturing of carapace to distinguish it from the Asian Giant Softshell Turtle *Pelochelys cantorii* Gray, 1864b. No geographic variation has been reported within the species' restricted range and no subspecies have been named. Relationship to and distinction from *Pelochelys cantorii* and *P. bibroni* warrant further investigation and documentation.

Distribution: Lowlands of New Guinea extending from the Madang region of Papua New Guinea (Sepik and Ramu drainages) to Wanggar River (Nabire region, southern shore of Cenderawasih Bay) in West Papua, Indonesia.

Suborder Pleurodira Cope, 1864

Family Chelidae Gray, 1825

A family of aquatic and semi-aquatic turtles containing about 55 species in 15 genera, of which 7 genera and 32 species are endemic to Australia, New Guinea, Timor and Roti (Fritz & Havaš, 2007; modified, this work). The remaining members of the family are restricted to South America, and fossil forms are not known outside their current range. As such, they are of undisputed Gondwanan origin. Pleurodirous (head and neck withdrawn sideways into shell); carapace and plastron rigid (plastron mildly kinetic in *Pseudemydura umbrina*), overlaid by distinct epidermal scutes; mesoplastral bones absent; forelimbs and hindlimbs with distinct ankle-joints (not paddle-shaped) and four or five claws on distinct webbed feet.

Key to Genera

- 1 Forelimbs each with five claws; gular scutes separated by the intergular; intergular scute in broad contact with the anterior margin of the plastron..... 2
- Forelimbs each with four claws; gular scutes in contact; intergular scute not in broad contact with the anterior margin of the plastron ***Chelodina***
- 2 Intergular scute not in contact with the pectoral scutes 3
- Intergular scute contacts and partly separates the pectoral scutes ***Pseudemydura***
- 3 Suture between the second and third costal scutes contacting the seventh marginal scute; suture between the third and fourth costal scutes contacting the ninth marginal scute 4
- Suture between the second and third costal scutes contacting the sixth marginal scute; suture between the third and fourth costal scutes contacting the eighth marginal scute ***Rheodytes***
- 4 Surface of the temporal region covered with distinct regular scales or low tubercles; dorsal surface of the head with a prominent head shield which may be entire or fragmented; cervical scute present or absent 5
- Skin of the temporal region smooth, sometimes broken into regular scales of low relief; dorsal surface of head without a prominent head shield; cervical scute present (except as a rare variant) ***Emydura***
- 5 Preloacal tail length greater than postloacal length only in adult males; tail round in cross section; cloacal orifice round; tail always shorter than half of carapace length 6
- Tail distinctive and large; preloacal length greater than postloacal length at all ages in both sexes; tail laterally

- compressed; cloacal orifice a longitudinal slit; tail up to 53% of carapace length in adult males *Elusor*
- 6 Prominent alveolar ridge on the triturating surfaces of the mouth; cervical scute absent (except as a rare variant); no prominent process of the head shield extending down the parietal ridge toward the tympanum *Elseya*
- Alveolar ridge absent; cervical scute absent in Australian species (except as a rare variant), present in New Guinea species (except as a rare variant); posterior process of the head shield extends laterally down the parietal ridge toward the tympanum *Myuchelys*

Genus *Chelodina* Fitzinger, 1826 (Long-necked and Snake-necked Turtles)

- 1794 *Chelodina longicollis* (Shaw, 1794), type species by original designation.
- 1828 *Hydraspis* Bell, 1828b. Type species *Chelodina longicollis* (Shaw, 1794).
- 1846 *Chelydina* Agassiz, 1846. Type species *Chelodina longicollis* (Shaw, 1794).
- 1894 *Chelydura* Oudemans, 1894. Type species *Chelodina longicollis* (Shaw, 1794).
- 1894 *Chelidura* Oudemans, 1894. Type species *Chelodina longicollis* (Shaw, 1794).
- 1985 *Macrochelodina* Wells & Wellington, 1985. Type species *Chelodina rugosa* Ogilby, 1890 by subsequent designation (Iverson et al., 2001). Synonymy that of Georges and Thomson, this work; assigned lower rank of subgenus (see below).
- 1985 *Hesperochelodina* Wells & Wellington, 1985, nomen nudum following Iverson et al., (2001).
- 2007 *Macrodiremys* McCord & Ouni, 2007a. Type species *Macrodiremys oblonga* sensu McCord & Ouni, 2007a = *Chelodina colliei*. Synonymy that of Georges and Thomson, this work; assigned lower rank of subgenus (see below).

A genus of turtles with exceptionally long necks; head and neck, when extended, typically as long or longer than the carapace; gular scutes meet in front of the intergular scute, or if not, barely separated by the intergular (common variant in *C. burrungandjii*); temporal arch absent from skull; four claws on front and back feet.

Three subgeneric groups within *Chelodina* have long been recognized (Burbidge, 1967; Burbidge et al., 1974; Georges et al., 2002) and referred to as (a) the *Chelodina longicollis* group (comprising *C. longicollis*, *C. novaeguineae* and *C. steindachneri*), (b) the *Chelodina expansa* group (comprising *C. expansa* and *C. rugosa*) and (c) *Chelodina colliei* (then referred to as *C. oblonga*). Goode (1967) retained the first group as Group A taxa and combined *C. colliei*, *C. expansa* and *C. rugosa* into Group B taxa, which has since been widely used (Legler, 1981). Unfortunately, Goode's Group B is not a natural phylogenetic unit. *C. colliei* of Group B is sister to the *Chelodina longicollis* group (Group A) despite its superficial resemblance to species of the *Chelodina expansa* group (Georges & Adams, 1992; Seddon et al., 1997; Georges et al., 1998). Thus, Goode's Group B, assigned by Iverson et al. (2001) to the name *Macrochelodina* made available by Wells and Wellington (1985), is paraphyletic—the common ancestor of *C. expansa* and *C. colliei* has *C. longicollis* among its descendents (Georges & Adams, 1992; Seddon et al., 1997; Georges et al., 1998). The three subgeneric groups, initially identified but not named by Burbidge and his colleagues, are natural (monophyletic) units.

The widespread and frequent reference in the literature to subgroups or major clades within the genus *Chelodina*, either in the sense used by Burbidge et al. (1974) or that of Goode (1967), suggests that they have some utility. Wells and Wellington (1985) defined *Macrochelodina* as a genus, but in the two decades that followed, its use was largely restricted to hobbyists and turtle fanciers (but see Fritz & Havaš, 2007). Wells and Wellington (1985) presented no satisfactory analysis to demonstrate that it was a valid taxon or a necessary change, and the change was self-printed without the benefit of scientific peer review. Their new genus served no clear purpose, in that there was no unacceptable paraphyly that needed to be resolved and indeed, were it not for the earlier mistake by Goode (1967), they would have created a paraphyly. Recognition of *Macrochelodina* at the level of genus would place in different genera, species that undergo widespread and common natural hybridization in Australia to yield viable and fertile offspring in the wild (e.g. *C. rugosa* and *C. canni*). Creation of the genus *Macrochelodina* to the exclusion of *C. colliei* would contribute toward the unwelcome proliferation of monotypic genera by encouraging the establishment of a monotypic genus for *C. colliei* (McCord & Ouni, 2007a). These are all considerations against the recognition of *Macrochelodina* as a genus and for which it is difficult to find a counterbalancing argument. For these reasons, we adopt the three long-standing subgeneric divisions of Burbidge et al. (1974), by lowering the rank of *Macrochelodina* to a subgenus of *Chelodina*, separating out *C. colliei* as a monotypic subgenus to resolve the paraphyly, and assigning existing available names to the subgenera.

Key to subgenera and species⁴

- 1 Plastron broad, covering or almost covering the anterior orifice of the shell in ventral view; intergular scute approximately twice as long as the suture between the pectoral scutes; length of head and neck equal or slightly less than length of the carapace; dorsum of neck with many blunt conical tubercles; fluid with a pungent odour secreted from ducts in the inguinal and axillary pockets when distressed subgenus *Chelodina*..... **2**
- Plastron narrow, covering only about half of the anterior orifice of the shell in ventral view; intergular scute approximately the same length as or shorter than the suture between the pectoral scutes; head and neck longer than carapace; dorsum of neck lacking obvious tubercles; fluid from ducts in the inguinal and axillary pockets if with noticeable odour, not pungent **8**
- 2 Expanded anterior lobe of the plastron moderate, not completely covering the anterior orifice of the shell in ventral view; sutures of plastron not edged with black, or at most narrowly edged with black; posterior marginal scutes not elevated medially to accommodate the tail **3**
- Expanded anterior lobe of the plastron very broad, covering the anterior orifice in ventral view (and all soft parts when withdrawn); sutures of the cream or yellow plastron broadly edged with black; posterior marginal scutes elevated medially to accommodate the tail *longicollis*
- 3 Carapace strongly convex, distinctly oval in outline **4**
- Carapace very flat, almost circular in outline *steindachneri*
- 4 First and second marginal scutes approximately equal in size **5**
- Second marginal scute distinctly larger than the first *mccordi*
- 5 Jaws and associated triturating surfaces robust **6**
- Jaws and associated triturating surfaces petite (as in *C. longicollis*) *pritchardi*
- 6 Head moderate, without distinct convexity to the dorsum of the head **7**
- Head robust, disproportionately large, with distinct convexity of the dorsum of the head *reimanni*
- 7 Northern Australia *canni*
- New Guinea *novaeguineae*
- 8 Carapace approximately oval; plastron of moderate length, less than twice as long as its width measured anterior to the bridge subgenus *Macrochelodina*..... **9**
- Carapace very narrow, plastron long, narrow, more than twice as long as its width measured anterior to the bridge... subgenus *Macrodiremys*..... *colliei*
- 9 Ventral surface of the cervical scute longer than wide, or length and width approximately equal **10**
- Ventral surface of the cervical scute much shorter than it is wide **11**
- 10 Distinct white patch immediately above and behind the tympanum, with or without dark blotches; ventral surface of the cervical scute longer than wide *parkeri*
- No distinctive white patches on the head; length and width of ventral surface of the cervical scute approximately equal *expansa*
- 11 Width of head moderate, not dramatically wider than the neck; two barbels on the chin, if present *rugosa*
- Head very broad, dramatically wider than the neck, multiple prominent barbels forming a linear series on each mandible *burrungandjii*

Subgenus *Chelodina* Fitzinger, 1826 (Long-necked Turtles)

1826 *Chelodina* (*Chelodina*) Fitzinger, 1826, nominotypical subgenus, established by Georges and Thomson, this work.

Length of head and neck equal to or slightly less than length of the carapace; plastron broad, covering or almost covering the anterior orifice of the shell in ventral view; length of intergular scute approximately twice that of the suture between the pectoral scutes; dorsum of neck with many blunt conical tubercles; fluid with a pungent odour secreted from ducts in the inguinal and axillary pockets when distressed.

Chelodina canni McCord & Thomson, 2002 (Canns Long-necked Turtle)

1985 *Chelodina rankini* Wells & Wellington, 1985, *nomen nudum*⁵ following Iverson et al. (2001).

2002 *Chelodina canni* McCord & Thomson, 2002, holotype, NTM 24515, from Malogie Waterhole, near Scarlet Hill on Kalala Station (16°08'S, 133°36'E), Northern Territory, Australia.

2008 *Chelodina novaeguineae canni*—Artnier, 2008.

4. This key does not follow phylogeny at the level of subgenus, owing to convergence in body form of *Chelodina* (*Macrodiremys*) *colliei* and species of *Chelodina* (*Macrochelodina*).

Species status uncontroversial, adequate description and diagnosis provided in the original description. Very closely related to *Chelodina novaeguineae* from New Guinea. Allozyme data not sufficient on their own to establish the species distinction between *C. canni* and *C. novaeguineae* (Georges et al., 2002). Queensland populations east of the Great Dividing Range are regarded as distinctive by Cann (2008), under the name *Chelodina rankini* and citing the privately circulated works of Wells (2007b), but there is no science to support the distinction. No diagnostic characters to distinguish the two emerged from allozyme comparisons (Georges et al., 2002). Freely hybridizes with *C. longicollis* to yield viable and fertile offspring in the Styx River of central coastal Queensland (Georges et al., 2002). No subspecies are recognised.

Distribution: From the Roper River drainage (Northern Territory) in the West, throughout the rivers draining into the Gulf of Carpentaria, and the east coast rivers south to the Styx River in central coastal Queensland.

***Chelodina longicollis* (Shaw, 1794) (Eastern Long-necked Turtle)**

- 1794 *Testudo longicollis* Shaw, 1794, holotype, not specified but presumed to be BMNH 1947.3.5.86 (Cogger et al., 1983), from unspecified locality.
- 1835 *Chelodina novaehollandiae* Duméril & Bibron, 1835, holotype, MNHP 6969, from Australia. Synonymy follows that of Boulenger (1889), Mertens and Wermuth (1955) and Wermuth and Mertens (1961).
- 1826 *Chelodina longicollis* - Fitzinger, 1826. First use of combination.
- 1855 *Chelodina sulcifera* Gray, 1855, holotype, BMNH 1947.3.5.87, from Australia. Synonymy follows that of Goode (1967).
- 1856 *Chelodina sulcata* Gray, 1856 [lapsus for *Chelodina sulcifera* Gray, 1855]. Synonymy follows that of Goode (1967).

Species status uncontroversial. Supported as a distinct and well-defined taxon by diagnostic allozyme characters (Georges & Adams, 1992; Georges et al., 2002). Major mitochondrial haplotype clades distinguishing populations east of the Great Dividing Range from most populations west of the range (Hodges, unpubl. data), not regarded as warranting recognition at the level of species or subspecies because the haplotypes do not each occur in a discrete geographic region. The coastal haplotype crosses the range in the New England Tablelands region, so the eastern and western populations are not diagnosable taxa based on mtDNA. Hybridizes with *Chelodina canni* to yield viable and fertile offspring where the two species come into contact (Styx River region) (Georges et al., 2002). No subspecies are recognised.

Distribution: Murray-Darling, coastal rivers and larger offshore islands from Eyre Peninsula west of Adelaide in South Australia to the Burdekin drainage of Queensland, headwaters of Cooper Creek drainage, Bulloo and Paroo drainages. Populations in northwest Tasmania, presumed introduced.

***Chelodina mccordi* Rhodin, 1994b (McCords Long-necked Turtle)**

- 1994 *Chelodina mccordi* Rhodin, 1994b, holotype, MCZ 176730, from western Timor, originally collected on Roti Island, East Nusa Tenggara Province, Indonesia.
- 2007 *Chelodina timorensis* McCord et al., 2007a, holotype, AMNH, R160135, swamps of Lake Ira Lalaro, East Timor. Synonymy follows that of Kuchling et al. (2007), Georges and Thomson, this work.

Adequate description and diagnosis provided in the original description (Rhodin, 1994b), with additional detail provided by Rhodin et al. (2008a). Allozyme data support the species designation (Georges et al., 2002). Specimens recently discovered on Timor (Kuchling et al., 2007) were named as a separate species (*Chelodina timorensis* McCord et al., 2007a) in the hobbyist literature, but brought into synonymy with *Chelodina mccordi* when described as a subspecies *Chelodina mccordi timorlestensis* in the peer reviewed literature (Kuchling et al., 2007). We recognize only one East Indian species in *Chelodina mccordi*

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5. Redescribed by Wells (2007b) under the same name in an attempt to meet the provisions of the Code, but the account appears in a privately prepared and circulated document that does not, in the opinion of the authors, meet the provisions of ICZN Articles 8 and 9 and Recommendation 8D and so is not considered a publication for the purposes of nomenclature. Even so, *Chelodina canni* now has precedence and there has been no evidence presented that the two names, if both were available, would represent two taxa.

comprising populations from the islands of Roti and Timor each of which, as divergent island forms, represent both *Diagnosable Terminal Taxa* and *ESUs* by the definitions outlined above. Kuchling et al. (2007) named these as subspecies—*Chelodina mccordi timorlestensis* Kuchling et al., 2007, holotype, WAM 165888, from Lake Iralalero, Timor-lesste, restricted to Timor-lesste and *Chelodina mccordi mccordi* restricted to Roti Island. McCord et al. (2007b) further distinguishes a third subspecies -- *Chelodina mccordi roteensis* holotype, AMNH R160132, from Lake Enduy, eastern Rote Island, Indonesia.

Distribution: The island of Rote, Indonesia, and the island of Timor, Timor Leste.

***Chelodina novaeguineae* Boulenger, 1888 (New Guinea Long-necked Turtle)**

1888 *Chelodina novaeguineae* Boulenger, 1888, syntypes (2), MCG C.E. 8407; BMNH 1946.1.22.36, from Mawatta, Binaturi River, Papua New Guinea.

2007 *Chelodina gunaleni* McCord & Ouni, 2007b, holotype, AMNH R160133, from a swamp of the Uta River basin, southern coastal Papua, Indonesia. Synonymy that of Georges and Thomson, this work.

Poorly known. Morphological data additional to that in the original description are provided by Rhodin (1994a). Very closely related to *Chelodina canni* from Australia (Georges et al., 2002); allozyme data insufficient on their own to establish the species distinction between *C. canni* and *C. novaeguineae*. Regarded by some as a species complex (Rhodin & Genorupa, 2000; McCord & Ouni, 2007b) but evidence in support of species designations within this suspected complex, including *Chelodina gunaleni* McCord & Ouni, 2007b, has not yet appeared in the peer reviewed scientific literature.

Distribution: Southern New Guinea.

***Chelodina pritchardi* Rhodin, 1994a (Pritchards Long-necked Turtle)**

1994 *Chelodina pritchardi* Rhodin, 1994a, holotype, MCZ 173543, from Bore, Kemp Welch River, 13 km SE of Kwikila, Central Province, Papua New Guinea.

Species status uncontroversial, adequate diagnosis and description provided in the original account (Rhodin, 1994a). Allozyme data support the species designation (Georges et al., 2002). No substantive geographic variation has been reported and no subspecies are recognised.

Distribution: Southern Papua New Guinea, from Laloki River in the west (range extension, this work) to Kemp Welch River in the east.

***Chelodina reimanni* Philippen & Grossman, 1990 (Reimanns Long-necked Turtle)**

1990 *Chelodina reimanni* Philippen & Grossman, 1990, holotype, MTD 29178, Merauke River, West Papua, Indonesian New Guinea.

2003 *Chelodina novaeguineae reimanni*—Artner, 2003.

In addition to the morphological evidence provided in the original description, morphological data supporting its status as a separate species were provided by Rhodin (1994a). Specimens used in allozyme comparisons were not distinct from *C. novaeguineae*, but they were from a captive collection, and may have been misidentified—further investigation is warranted. No substantive geographic variation has been reported and no subspecies are recognised.

Distribution: Southeastern West Papua, Indonesia, and adjacent Papua New Guinea.

***Chelodina steindachneri* Siebenrock, 1914 (Steindachners Long-necked Turtle)**

1914 *Chelodina steindachneri* Siebenrock, 1914, holotype, NHMW 19798, from Marloo Station, Grey River, Western Australia.

1923 *Chelodina millymillyensis* Glauert, 1923, lectotype, WAM R1000, Milly Milly Creek, Milly Milly Station, Murcheson River, Western Australia, designated by Cogger et al. (1983). Synonymy follows that of Mertens and Wermuth (1955) and Wermuth and Mertens (1961).

Uncontroversial. Allozyme data support the species designation (Georges et al., 2002). No substantive geographic variation has been reported and no subspecies are recognised.

Distribution: Middle-west of Western Australia from the DeGrey drainage in the north to the Murchison drainage in the south, west to Wiluna, Salt Lake drainage.

Subgenus *Macrochelodina* Wells & Wellington, 1985 (Snake-necked Turtles)

1985 *Chelodina* (*Macrochelodina*) (Wells & Wellington, 1985), rank reduced from genus to subgenus by Georges and Thomson, this work.

Carapace broadly oval with noticeable flaring in the vicinity of marginal scutes 8–10; plastron narrow, covering only about half of the anterior orifice of the shell in ventral view; plastron of moderate length, less than twice as long as its width measured anterior to the bridge; head and neck longer than carapace; length of intergular scute approximately equal to or shorter than that of the suture between the pectoral scutes; dorsum of neck finely reticulated, lacking obvious tubercles; fluid from ducts in the inguinal and axillary pockets with noticeable odour, but not pungent.

Macrochelodina is an available name under the Code and *Chelodina rugosa* Ogilby, 1890 was fixed as the type species, in accordance with Articles 67.9 and 70.3 of the Code (Iverson et al., 2001) and following the presumed intent of Wells and Wellington (1985). Wells and Wellington had chosen *C. oblonga* as the type species for their new genus, but the holotype for *C. oblonga* had been misidentified (Thomson, 2000; 2006). When Goode (1967) restricted *C. oblonga* to the southwestern form and resurrected *C. rugosa* (as *C. siebenrocki*) for the widespread northern form, he was in error. The holotype of what Goode regarded as *C. oblonga* is a specimen of what we currently regard as *C. rugosa* (Thomson, 2000; Thomson, 2006). The name *Macrochelodina* as defined by Wells and Wellington (1985) is thus available, ironically, for the *Chelodina expansa* group of Burbidge et al. (1974), to which it is now assigned.

***Chelodina burrungandjii* Thomson et al., 2000 (Sandstone Snake-necked Turtle)**

2000 *Chelodina burrungandjii* Thomson et al., 2000, holotype, NTM 16010, Koolpin Gorge, South Alligator River (13°28'S, 132°38'E).

2003 *Macrochelodina burrungandjii*—Artner, 2003.

2007 *Macrochelodina walloyarrina* McCord & Ouni, 2007a, holotype, WAM R164345, from the Fitzroy River, at Fitzroy River Crossing, Western Australia, Australia. Synonymy that of Georges and Thomson, this work.

Adequate description and diagnosis provided in the original account (Thomson et al., 2000). Additional information provided by Thomson et al. (2009). Allozyme data support the species designation (Georges et al., 2002). Kimberley populations are regarded by some as distinctive (Cann, 1998; Thomson et al., 2000; McCord & Ouni, 2007a; Cann, 2008), but resolution of this is complicated by issues of hybridization and introgression—*C. burrungandjii* hybridizes with *C. rugosa* yielding fertile offspring where they come in contact, typically in the escarpment country bordering the sandstone tablelands and the lowlands (Georges et al., 2002). *C. rugosa* mitochondrial haplotype appears to have swept through the Arnhem Land populations of *C. burrungandjii* (Alacs, 2008). Artner (2008) distinguishes the Arnhem Land and Kimberley forms as subspecies *Chelodina burrungandjii burrungandjii* and *Chelodina burrungandjii walloyarrina*, respectively.

Distribution: Permanent pools in the rivers draining the Arnhem Land and Kimberley sandstone plateaus, including the plunge pools of the associated escarpments.

***Chelodina expansa* Gray, 1857 (Broad-shelled Turtle)**

1857 *Chelodina expansa* Gray, 1857, syntypes, BMNH 1947.3.4.21, BMNH 1947.3.5.88, from Australia.

1969 *Chelodina oblonga expansa*—Blackmore, 1969.

1985 *Macrochelodina expansa*—Wells & Wellington, 1985.

Taxon uncontroversial. Allozyme data support the species designation (Georges et al., 2002). Three major mitochondrial haplotype clades distinguishing populations of the Murray-Darling drainage from those of coastal Queensland (Hodges, unpubl. data), not regarded as warranting recognition at the level of species or subspecies there being no corroborative morphological analysis. No substantive geographic morphological variation has been reported and no subspecies are recognised.

Distribution: Murray-Darling, coastal Queensland from the Logan-Albert drainage in the south to the Fitzroy drainage in the north, including Fraser, Stradbroke and Moreton Islands.

***Chelodina parkeri* Rhodin & Mittermeier, 1976 (Parkers Snake-necked Turtle)**

1976 *Chelodina parkeri* Rhodin & Mittermeier, 1976, holotype, AMS 21425, from Mawa, Lake Murray, Western District, Papua New Guinea.

Taxon uncontroversial, with adequate description and diagnosis provided in the original account (Rhodin & Mittermeier, 1976). Has not been assessed using DNA or allozyme evidence. No subspecies are recognised.

Distribution: Floodplains of the Bamu-Aramia and Fly River drainages. No substantive geographic variation has been reported.

***Chelodina rugosa* Ogilby, 1890 (Northern Snake-necked Turtle)**

1841 *Chelodina oblonga* Gray, 1841, holotype, BMNH 1947.3.5.89, from Western Australia. Synonymy follows that of (Thomson, 2000; 2006).

1890 *Chelodina rugosa* Ogilby, 1890, holotype, AMS R6256, from Cape York, Queensland. Precedence over *Chelodina oblonga* pending outcome of Case 3351, ICZN (Thomson, 2006).

1901 *Chelodina siebenrocki* Werner, 1901, holotype, ZMB 16491, from Papua New Guinea. Synonymy follows that of Georges et al. (2002), Georges and Thomson (2006)..

1915 *Chelodina intergularis* Fry (1915), holotype, AMS R6255, from Australia. Synonymy follows that of Wermuth and Mertens (1961) and Cogger et al. (1983).

1969 *Chelodina oblonga rugosa*—Blackmore, 1969.

1969 *Chelodina oblonga siebenrocki*—Blackmore, 1969.

1985 *Macrochelodina billabong* Wells & Wellington, 1985, *nomen nudum*⁶ following Iverson et al. (2001).

1985 *Macrochelodina rugosa*—Wells & Wellington, 1985.

1997 *Chelodina kuchlingi* Cann, 1997c, holotype, WAM R29411, from Kalumburu, NW Australia, (14.18'S, 126.28'E). Synonymy follows that of Georges and Thomson (2006).

Synonymised with *C. oblonga* by Siebenrock (1909). Northern populations of *C. oblonga* referred to *C. rugosa* by Goode (1967) in error. Name *Chelodina rugosa* retained under Article 23.9.3 of the Code (Thomson, 2006: Case 3351, pending). Allozyme data support the species designation (Georges et al., 2002), though hybridization with other species common. Two major mitochondrial haplotype clades distinguishing populations from the Northern Territory from those of southern New Guinea, Cape York and the rivers flowing into the Gulf of Carpentaria (Alacs, 2008), not regarded as warranting recognition at the level of species or subspecies. Hybridizes with *C. canni* to yield fertile offspring where the two come in contact (Georges et al., 2002); hybridizes with *C. burrungandjii* in the Arnhem Land region leading to widespread introgression of the *C. rugosa* haplotype in *C. burrungandjii* (Alacs, 2008). *Chelodina kuchlingi* Cann, 1997c was described from a single specimen of uncertain origin with a long history of captivity and so is treated as a junior synonym of *C. rugosa* (Georges & Thomson, 2006). *Chelodina siebenrocki* is morphologically and genetically indistinguishable from populations of *Chelodina rugosa* from Cape York Peninsula, Australia (Georges et al., 2002; Georges & Thomson, 2006). Artner (2008) distinguishes the New Guinea form as a named subspecies, *Chelodina rugosa siebenrocki* Werner, 1901.

Distribution: Coastal drainages from Victoria River in the west to the rivers draining east and west on Cape York, south to the Normanby drainage in the east; coastal tea tree swamps of southern New Guinea.

Subgenus *Macrodiremys* McCord & Ouni, 2007a (Oblong Turtle)

1985 *Chelodina (Macrodiremys)* (McCord & Ouni, 2007a), rank reduced from genus to subgenus by Georges and Thomson, this work.

Head and neck, when extended, longer than carapace; carapace very narrow, oval with negligible flaring posteriorly; plastron long, narrow, more than twice as long as its width measured immediately anterior to the bridge, covering only about half of the anterior orifice of the shell in ventral view; dorsum of neck finely reticulated, lacking obvious tubercles. Monotypic.

6. There is no evidence that the populations of the Northern Territory represent a different species from those of the type locality for *C. rugosa* (Cape York) (but see Alacs, 2008), and even were this to be so, the name *C. oblonga* would take precedence (Thomson, 2006).

Macrodiremys is a second genus erected in the hobbyist literature, and in a fashion that requires remediation of the type species if the intent of the original authors (McCord & Ouni, 2007a) is to be met. A strict reading of the Code would have *Macrodiremys* based on the nominal species *C. oblonga* (a synonym of *C. rugosa*), and thus a junior synonym of *Macrochelodina*. This was clearly not the intent of McCord and Ouni (2007a). Under Article 67.13.1 of the Code, if an author fixes, as the type species of a new nominal genus, a species originally included in a previously established name by an earlier author by virtue of a misidentification or misapplication, the type species fixed by that action is deemed to be a new nominal species. Thus *Chelodina oblonga* McCord & Ouni, 2007a is a homonym of *Chelodina oblonga* Gray, 1841, and a junior synonym of *C. colliei*. The type species of *Macrodiremys* is *C. oblonga* McCord & Ouni, 2007a (non *C. oblonga* Gray, 1841) = *C. colliei* Gray, 1856. The name *Macrodiremys* stands with *Chelodina colliei* Gray, 1856 as the type species.

***Chelodina colliei* Gray, 1856 (Oblong Turtle)**

1856 *Chelodina colliei* Gray, 1856, lectotype, BMNH 1947.3.5.91 (Thomson, 2000), from Swan River, Australia.

2007 *Chelodina oblonga* McCord & Ouni, 2007a [non *Chelodina oblonga* Gray, 1841, homonym]. Synonymy that of Georges and Thomson, this work.

Regarded as a junior synonym of *C. oblonga* by Boulenger (1889) which at the time included what we now regard as *C. rugosa* (including *C. siebenrocki*). *Chelodina colliei* restricted to *C. oblonga* by Goode (1967) in error (Thomson, 2000; 2006). Allozyme data support the species designation (Georges et al., 2002). McCord and Ouni (2007a) attempted to assign a specimen of this species as a neotype for *C. oblonga*, but their action was invalid under the Code, because a type specimen already exists. This has been rectified by Georges and Thomson, present work, as outlined in the genus account above. No substantive geographic variation has been reported and no subspecies are recognised.

Distribution: South western Western Australia.

Genus *Elseya* Gray, 1867 (Australasian Snapping Turtles)

1863 *Elseya dentata* (Gray, 1863), type species by subsequent designation, Lindholm (1929).

A genus of large river-turtles with moderately long necks, with head and neck, when extended, much shorter than the carapace; gular scutes entirely separated by the intergular scute; prominent alveolar ridge on the triturating surfaces of the jaw sheaths; cervical scute absent (except as a rare variant); a horny casque (head shield) on top of the head of adults, entire, fragmented or deeply fenestrated; no prominent process of the head shield extending down the parietal ridge toward the tympanum; temporal region covered with prominent scales; temporal stripes absent; eye dark and lacking contrast; front feet with five claws, rear with four claws. The genus *Elseya* has a chequered history. It was initially erected for *Elseya dentata* and *Myuchelys latisternum* (Gray, 1867) with *E. dentata* (Gray, 1863) later designated as the type species (Lindholm, 1929). Boulenger (1889) redefined the genus as being characterised by the alveolar ridge, a longitudinal ridge on the maxillary triturating surface, present only in *E. dentata*. *Myuchelys latisternum* and *M. novaeguineae* were placed in the genus *Emydura*. Goode (1967) expressed little faith in the alveolar ridge as a taxonomic feature at the generic level, citing cases of variation in this feature among species of well recognised cryptodiran turtle genera, and transferred *M. latisternum* and *M. novaeguineae* back to *Elseya*. Gaffney (1979) treated *Elseya* as a junior synonym of *Emydura*, with support from Frair (1980: serology) and McDowell (1983: morphology). Georges and Adams (1992) using molecular approaches demonstrated that *Myuchelys latisternum* and three other species formed a clade paraphyletic with respect to the remaining species of *Elseya*—their common ancestor has *Emydura* among its descendents. While this result concurred with that of McDowell (1983), we believe that the paraphyly is best resolved by splitting the genus *Elseya* (foreshadowed by Legler, 1981) rather than adopting the sweeping synonymy recommended by McDowell and Gaffney. We therefore restrict the genus *Elseya* to include only the species *E. dentata* (type species), *E. irwini*, *E. lavarackorum*, *E. albagula* and *E. branderhorsti*, diagnosed by the presence of an alveolar ridge on the maxillary triturating surface (Boulenger, 1889) together with the other characters outlined above. Although

mitochondrial sequence data suggest two major clades within the genus (Georges, unpubl. data), no subgenera are considered necessary.

Key to species

Elseya lavarackorum could not be placed in the key owing to insufficient diagnostic morphological characters evident in the live animal. Distribution poorly known. *Elseya dentata* [Johnstone] (Georges & Adams, 1996) considered conspecific with *Elseya irwini*.

- 1 Anterior carapace expanded, squared off, anterior extent of second marginal scute as great or greater than that of first marginal scute in adults Queensland clade ...**2**
 - Carapace broadly oval, anterior extent of carapace greatest at first marginal scute in adults Northern clade...**3**
- 2 Dorsal surface of skull and overlying head shield smooth; anterior carapace squared off, extent of second marginal scute equal to or greater than that of first marginal scute in adults; prominent white or cream markings on throat and sides of head may extend to cover the dorsal surface of head in adult females (Burdekin drainage only) *irwini*⁷
 - Dorsal surface of the skull and overlying head shield deeply fenestrated in full grown adults; anterior carapace ovoid, first marginal scute the most anterior scute of the carapace; prominent white or cream markings on throat and sides of head, not extending to dorsal surface of head..... *albagula*
- 3 Plastron cream or white, unblemished by streaks, darker borders of the scute sutures, or other darker markings; scales on temporal region of head not prominent; side of head often with white or cream blotches **4**
 - Plastron yellow, cream or white, with streaks of brown or black, darker borders to the scutes or other darker markings (after removal of any staining) *dentata*
- 4 Plastron of low relief, little or no abrupt angle between the bridge and the ventral surface of the plastron; head shield fragmented *Elseya dentata* [South Alligator]⁸
 - Ventral surface of the plastron at a distinct angle from the bridge; head shield entire *branderhorsti*

Elseya albagula Thomson et al., 2006 (White-throated Snapping Turtle)

2006 *Elseya albagula* Thomson et al., 2006, holotype, QM J781785, plunge pool at the downstream side of Ned Churchwood Weir (25°03'S 152°05'E), Burnett River, Queensland, Australia.

2008 *Elseya dentata albagula*—Artner, 2008.

Uncontroversial. Allozyme evidence of species status provided by Georges and Adams (1992; 1996) who identified a series of highly divergent entities within what was then regarded as *Elseya dentata*. Species status assigned on the basis of divergence in comparison with that between well established species. Morphological data used to define the species provided in the original description (Thomson et al., 2006). Additional morphological data provided by Cann (1998:190-191); additional molecular data provided by Farley et al. (2007). No subspecies are recognised.

Distribution: Mary, Burnett and Fitzroy drainages of eastern Queensland.

Elseya branderhorsti (Ouwens, 1914) (New Guinea Snapping Turtle)

1914 *Emydura branderhorsti* Ouwens, 1914, described from a live specimen, type either non-existent or lost (Leo Brongersma *pers. comm.* to John Goode 1967, 28 June 1963), from southern New Guinea.

1994 *Elseya branderhorsti*—Bour et al., in David, 1994. First use of combination.

Commonly confused with *Myuchelys novaeguineae* because of its superficial resemblance. Original description states lack of a cervical scute as the diagnostic character. Morphological diagnosis provided and status clarified by Georges et al. (2006). DNA sequence data suggest affinities with the species of *Elseya* from northern Australia (Georges, unpubl. data). No subspecies are recognised.

7. Includes *Elseya* sp. aff. *dentata* [Johnstone] *sensu* Georges and Adams (1996). *Elseya stirlingi* Wells & Wellington, 1985, a name applied to the Johnstone River form, is a *nomen nudum* (Iverson, et al., 2001). Wells (2007b) attempted a redescription under the same name, presumably to meet the provisions of the Code, but the account appeared in a document that does not, in the opinion of the authors, meet the provisions of ICZN Articles 8 and 9 and Recommendation 8D and so is not considered a publication for the purposes of nomenclature.
8. *sensu* Georges and Adams (1996). A manuscript with a formal description of this species is at a late stage (Thomson, in prep). Wells (2002b) attempted a description, as *Elseya jukesii*, but their taxon is a *nomen nudum* and the account appeared in a privately prepared and circulated document that does not, in the opinion of the authors, meet the provisions of ICZN Articles 8 and 9 and Recommendation 8D and so is not considered a publication for the purposes of nomenclature. His later account (Wells, 2007c) attempting to rectify the *nomen nudum* is not, for the same reasons, considered a publication for the purposes of nomenclature.

Distribution: Southern New Guinea, coastal rivers west of and including the Fly River. Not found in intensive turtle surveys of the Bamu-Aramia or Kikori drainages.

***Elseya dentata* (Gray, 1863) (Northern Snapping Turtle)**

- 1863 *Chelymys dentata* Gray, 1863, syntypes, BMNH 1947.3.6.3 (probably the holotype), BMNH 1947.3.6.2, from Beagles Valley, upper Victoria River, Northern Territory, Australia.
1864 *Chelymys elseyi* Gray, 1864a, *nomen nudum* following Fritz and Havaš (2007).
1867 *Elseya dentata*—Gray, 1867. First use of combination.
1870 *Chelymys elseya* Gray, 1870, *nomen nudum* following Wermuth and Mertens (1961).
1872 *Elseya intermedia* Gray, 1872a, holotype, BMNH 1947.3.4.14, from upper part of Victoria River, NT, Australia. Synonymy follows that of Cogger et al. (1983).

2000 *Elseya flaviventralis* Georges et al., 2000, *nomen nudum* following Fritz and Havaš (2007).
Type species for the genus *Elseya*. Substantially redefined by the descriptions of *E. albagula*, *E. irwini*, *E. lavarackorum* formerly regarded as parts of *E. dentata*. Further subdivision of the latter species may be forthcoming. A morphologically distinctive form occurs in Arnhem Land and is currently regarded as *E. dentata* but is genetically very distinct (*Elseya dentata* [South Alligator] (*sensu* Georges & Adams, 1996)). A description and diagnosis being prepared for publication through accepted channels by Scott Thomson. No subspecies are recognised.

Distribution: A river turtle occupying the northern Australian Macarthur drainage in the east to the Fitzroy drainage (Western Australia) in the west.

***Elseya irwini* Cann, 1997b (Irwins Snapping Turtle)**

- 1985 *Elseya stirlingi* Wells & Wellington, 1985, *nomen nudum*⁹, following Iverson et al. (2001).
1992 *Elseya* sp. "aff. *dentata* [Johnstone]" [= *Elseya dentata* in part] Georges, 1992.
1997 *Elseya irwini* Cann, 1997b, holotype, QM J59431, from Burdekin River (19°42'S 147°18'E), approximately 18 km upstream from Ayr, Queensland, Australia.
2008 *Elseya dentata irwini*—Artner, 2008.

First described in the magazine *Monitor*; not subject to peer review; later reproduced in a more widely available book (Cann, 1998). Diagnosis based on colouration, particularly the extent of light colour of the head which extends to cover the head shield. A distinctive form occurs in the Johnston drainage and Hartley Creek, north Queensland (*Elseya dentata* [Johnstone], *sensu* Georges & Adams, 1996). Genetic support for the distinction between the two is very weak, not sufficient on its own to separate the two as species, though together they are strongly divergent from all other taxa. Morphological differences between the two are minor, apart from frequency in coloration traits. No subspecies are recognised.

Distribution: Restricted to the Burdekin, Johnstone and Hartley Creek drainages, Queensland, Australia.

***Elseya lavarackorum* (White & Archer, 1994) (Gulf Snapping Turtle)**

- 1994 *Emydura lavarackorum* White & Archer, 1994, holotype, QM F24121, from Terrace Site, an excavation in fluvial sediments exposed on the south bank of the Gregory River, Riversleigh Station, northwestern of Mount Isa (Pleistocene), Queensland, Australia (18°35'S 138°35'E).
1997 *Elseya lavarackorum*—Thomson et al., 1997. First use of combination.
2008 *Elseya dentata lavarackorum*—Artner, 2008.

Description based on a partial carapace and associated plastron from the Pleistocene deposits of Riversleigh in Queensland. Thomson et al. (1997) reassigned the specimen to genus *Elseya* on the basis of comparisons between the fossil and an undescribed extant species identified in allozyme comparisons by Georges and Adams (1996). Geographic range is poorly known, and external morphological characters sufficient to clearly distinguish the species from other members of the genus *Elseya* are not available (but see Thomson et al., 1997). No subspecies are recognised.

Distribution: Poorly known. Nicholson River, Queensland.

9. Redescribed under the same name by Wells (2007c) in an attempt to meet the Code, but the document privately produced and circulated by Wells does not, in the opinion of the authors, meet the provisions of ICZN Articles 8 and 9 and Recommendation 8D and so is not regarded as a publication for nomenclatural purposes.

Genus *Elusor* Cann & Legler, 1994 (Mary River Turtle)

1994 *Elusor macrurus* Cann & Legler, 1994, type species by monotypy.

A genus represented by a single living species *Elusor macrurus* Cann & Legler, 1994 restricted to the Mary drainage of eastern Queensland, Australia. Moderately long neck, head and neck, when extended, much shorter than the carapace; border to carapace oval, smooth in adults, moderately serrated in juveniles; gular scutes entirely separated by the intergular scute; triturating surfaces of the jaw sheaths lacking a prominent alveolar ridge; cervical scute present (except as a rare variant); head with a horny casque (head shield); temporal region covered with prominent raised tubercles; blunt, low tubercles on the dorsal surface of the neck; no temporal stripe; tail distinctive and large (up to 53% of carapace length in adult males), laterally compressed; precloacal length greater than postcloacal length at all ages in both sexes; cloacal orifice a longitudinal slit; iris distinct; front feet with five claws, rear with four claws.

***Elusor macrurus* Cann & Legler, 1994 (Mary River Turtle)**

1994 *Elusor macrurus* Cann & Legler, 1994, holotype, QM J51275, from Mary River, 45.5 km S and 21.0 km W of Maryborough, Queensland, Australia (25°58'S, 152°30'E).

Uncontroversial. Original description adequate to establish status as a distinct species. Genetically very distinct (>19 allelic fixed differences [>37%] from other chelid taxa), with no clear affinities (Georges & Adams, 1992; 1996). Restricted to a single drainage; no subspecies are recognized.

Distribution: Restricted to the Mary drainage of south coastal Queensland, Australia.

Genus *Emydura* Bonaparte, 1836 (Australasian River Turtles)

1836 *Emydura* Bonaparte, 1836, type species *Emys macquaria* Cuvier, 1829 (*nomen nudum*)= *Chelys (Hydraspis) macquarri* Gray, 1831 by monotypy.

1844 *Chelymys* Gray, 1844, type species *Chelymys macquaria*=*Chelys (Hydraspis) macquarii* Gray, 1831 by monotypy. Synonymy follows that of Boulenger, (1889).

1871 *Euchelymys* Gray, 1871b by subsequent designation (Lindholm, 1929), type species *Euchelymys sulcifera* Gray, 1871b = *Hydraspis macquarii* Gray, 1831 = *Emydura macquarii* (Gray, 1830). Synonymy follows that of Boulenger (1889).

1985 *Tropicochelymys* Wells & Wellington, 1985, type species *Emydura victoriae* (Wells & Wellington, 1985). Synonymy follows that of Iverson et al. (2001).

A genus of turtles with moderately long necks, with head and neck, when extended, much shorter than the carapace; gular scutes entirely separated by the intergular scute; triturating surfaces of the jaw sheaths lacking a prominent alveolar ridge; cervical scute present (except as a rare variant); head rarely with a horny casque (head shield) except in older adults, and even then, without a discrete margin; temporal region smooth, not covered with prominent raised tubercles; a cream, yellow or red temporal stripes in most species; iris distinct; front feet with five claws, rear with four claws.

The genus *Elseya* has been variously defined depending on the definition of the genus *Elseya* (refer to the generic account for *Elseya* above). Boulenger (1889) redefined the genus to include *Myuchelys latisternum* and *M. novaeguineae*. Goode (1967) transferred *M. latisternum* and *M. novaeguineae* back to *Elseya*. Gaffney (1979) in a sweeping synonymy, treated *Elseya* as a junior synonym of *Emydura*, with support from Frair (1980) and McDowell (1983), but this has not been widely accepted. Molecular data support the monophyly of the genus *Emydura* as defined here (Georges & Adams, 1996). Mitochondrial sequence data suggests two major haplotype clades within the genus, corresponding to geography (Shaffer and Georges, unpubl. data), but no subgenera are considered necessary.

Key to species¹⁰

- 1 Triturating surfaces of maxillary sheath simple, not expanded to form a crushing plate on the roof of the mouth; length of mandibular symphysis in adults approximately equal to the horizontal diameter of the tympanum; post-ocular stripe absent, or if present, cream, yellow through to bright salmon, fading with age; iris with or without leading and trailing dark spots **2**
 - Triturating surfaces of the maxillary sheath expanded, meeting medially to form a crushing plate on the roof of the mouth; length of mandibular symphysis in adults about 1.5 times the horizontal diameter of the tympanum; post-ocular stripe typically bright red, fading with age; iris without leading and trailing dark spots; macrocephaly in adults common **victoriae**
- 2 Triturating surfaces of the maxillary and mandibular sheaths unremarkable, borders of the triturating surfaces of the maxillary sheath approximately parallel for their full length; facial stripe present or absent, if present, varies in color from cream, yellow, pink or bright salmon **3**
 - Moderate medial expansion of the triturating surfaces of the maxillary sheath; post-ocular stripe universally yellow (fading in older individuals); carapace commonly with distinct rugations in adult individuals; macrocephaly uncommon **tanybaraga**
- 3 Iris with leading and trailing dark spots; prominent facial stripe extending from the tympanum through the upper eyelid to the tip of the nose **subglobosa**
 - Iris clear, without leading and trailing dark spots; facial stripe present or absent, if present, as a cream or yellow post-ocular stripe only **macquarii**

Emydura macquarii (Gray, 1830) (Southern River Turtles)

Once thought to be restricted to the single, albeit large, Murray-Darling drainage, allozyme comparisons revealed no fixed differences among *Emydura macquarii*, *E. signata*, *E. krefftii* and other distinctive forms from Fraser Island (Queensland) and Cooper Creek (central Australia) (Georges & Adams, 1996). They shared even rare alleles. In the absence of consistent morphological characters to distinguish them, the latter were treated as junior synonyms by Georges (1994) and later designated as junior synonyms of *E. macquarii* (Georges & Adams, 1996). The five forms have since been treated as or further subdivided into subspecies (Cann, 1998; Cann et al., 2003; McCord et al., 2003). Mitochondrial sequence data further reveals a number of highly divergent mitochondrial haplotypes within the broader southern *Emydura* clade (*Emydura macquarii*) (Shaffer and Georges, unpubl. data). We synonymise those subspecies only where this is required to resolve overlap in concept (refer to the synonymy for *Emydura macquarii macquarii*), and retain and use those that have some currency in the literature and represent aggregates of populations in a contiguous series of drainages—*Emydura macquarii macquarii*, *E. m. emmotti*, *E. m. krefftii* and *E. m. nigra*.

Distribution: Coastal drainages from the Nepean-Hawkesbury drainage (New South Wales) in the south the the Normanby drainage (Queensland) in the Nouth; Murray-Darling drainage; Cooper, Diamantina, Paroo and Bulloo drainages of central Australia.

Key to subspecies

- 1 Distinct yellow or post-ocular stripe lacking in adults (except as a rare variant) **2**
 - Prominent yellow post-ocular stripe in adults; carapace rarely flared posteriorly; coastal Queensland drainages from Mary River in the south to Normanby River in the north ***E. m. krefftii***
- 2 Carapace varies from light to dark brown **3**
 - Carapace black or very dark brown; dorsal surface of head, neck and limbs black or very dark grey, melanistic; body size small, pygmy; Fraser Island and Cooloola Peninsula, Queensland ***E. m. nigra***
- 3 Carapace commonly widely flared posteriorly; body size moderate; Murray-Darling drainage, coastal drainages from the Nepean Hawkesbury in the south to the Brisbane and Pine Rivers drainages in the north, Paroo and Bullo drainages to the west ***E. m. macquarii***
 - Carapace at most moderately flared posteriorly; adult body size large, gigantism; Cooper Creek, Diamantina, Bulloo drainages in central east Australia ***E. m. emmotti***

10. *Emydura subglobosa worrelli* and *E. tanybaraga* cannot be distinguished reliably in the field, and the key is intended as a guide only.

— *Emydura macquarii macquarii* (Gray, 1830) (Macquarie River Turtle)

- 1829 *Emys macquaria* Cuvier, 1829 *nomen nudum*=*Chelys (Hydraspis) macquarii* Gray, 1830.
1830 *Chelys (Hydraspis) macquarii* Gray, 1830, holotype, MNHP 9409, from Australia, subsequently corrected to Macquarie River, New South Wales (Gray, 1831; 1872b).
1831 *Hydraspis macquarrii* Gray, 1831.
1841 *Hydraspis australis* Gray, 1841, holotype, BMNH 1947.3.4.36, from "Western Australia" later corrected to Macquarie River, New South Wales by Gray (1872b). Synonymy follows that of Cogger et al. (1983). See comment under *Emydura victoriae*.
1871 *Euchelymys sulcifera* Gray, 1871b, lectotype by subsequent designation (Cogger et al., 1983), BMNH 1947.3.5.97, from North Australia. Synonymy follows that of Goode (1967).
1932 *Emydura signata* Ahl, 1932, holotype, ZMB 34102, from Brisbane district, Queensland, Australia. Synonymy follows that of Georges and Adams (1996).
1969 *Emydura macquarii macquarii*—Blackmore, 1969 First use of combination.
1970 *Emydura canni* Worrell, 1970, *nomen nudum* following Wermuth and Mertens (1977).
1977 *Emydura macquarrii signata* —Wermuth & Mertens, 1977.
1985 *Chelymys cooki* Wells & Wellington, 1985, *nomen nudum* following Iverson et al. (2001).
1985 *Chelymys johncanni* Wells & Wellington, 1985, *nomen nudum* following Iverson et al. (2001).
1993 *Emydura macquarii signata*—Gosławski & Hryniewicz, 1993.
1998 *Emydura macquarii binjing* Cann, 1998, holotype, AMS R59558, from Clarence drainage, New South Wales (29°45'S, 152°15'E). Synonymy that of Georges and Thomson, this work.
1998 *Emydura macquarii dharra* Cann, 1998, holotype, AMS R59553, from Macleay River, New South Wales (30°54'S, 152°10'E). Synonymy that of Georges and Thomson, this work.
1998 *Emydura macquarii gunabarra* Cann, 1998, holotype, AMS 143596, from Hunter River, New South Wales (32°09'S, 150°58'E). Synonymy that of Georges and Thomson, this work.
1998 *Emydura macquarii dharuk* Cann, 1998, holotype, AMS 143598, from Nortons Basin, Nepean River, 0.5 km upstream from the junction of the Waragamba and Nepean Rivers (33°52'S, 150°37'E). Synonymy that of Georges and Thomson, this work.

A subspecies of southern *Emydura macquarii* that is distinguished by the usual absence of a yellow postocular stripe persisting into adulthood (usually present and persisting into adulthood in *Emydura macquarii krefftii*; variable in *E. m. emmotti* and *E. m. nigra*). *Emydura signata* Ahl, 1932 was described from two juvenile specimens and said to differ from *Emydura macquarii* by the serrated posterior margin of the carapace, but the level of serration on the holotype is slight (Ahl, 1932:127) and at this level of expression, is a highly variable character both developmentally and geographically in the *Emydura*. We therefore synonymize it with *Emydura macquarii macquarii* following Georges and Adams (1996). Similarly, the subspecies *Emydura macquarii macquarii* overlaps in concept with the subspecies of Cann 1998) leading to the synonymies listed above. Specimens of this subspecies vary in shell shape and dramatically in body size from drainage to drainage, interpreted as phenotypic responses to local conditions. No distinction could be established among populations *E. m. macquarii* as defined here using allozyme electrophoresis (Georges & Adams, 1996), though some coastal populations have deeply divergent mitochondrial haplotypes (Shaffer and Georges, unpubl. data). Populations from the Bellinger River regarded as distinctive and listed as endangered in the Reptile Action Plan (Cogger et al., 1993) are unremarkable genetically and almost certainly introduced to the drainage from adjacent drainages (Georges et al., 2007). Species status not warranted.

Distribution: Murray-Darling drainage, coastal rivers from the Hawkesbury-Nepean drainage in the south to the Brisbane and Pine Rivers drainages in the north, west in the Paroo and Bulloo drainages.

— *Emydura macquarii emmotti* Cann et al., 2003 (Cooper Creek Turtle)

- 1985 *Chelymys windorah* Wells & Wellington, 1985, *nomen nudum* following Iverson et al. (2001).
2003 *Emydura macquarii emmotti* Cann et al., 2003, holotype, QM J51255, from Waterloo Station, Shearing Shed Waterhole, south-western Queensland, Australia (24°13'S, 143°17'E).
2004 *Emydura emmotti*—Cann et al., 2003.

An inland form occupying the permanent waterholes of the Cooper Creek floodplain. It is distinguished from the other forms largely by its large body size and associated morphological and

ecological parameters and relatively light colour (fawn to light brown) of the carapace. Its distinctive features may be local adaptation and phenotypic responses to local conditions (particularly the sporadic oversupply of food, post-flooding) but this warrants further investigation. Not genetically distinct from other populations of *Emydura macquarii* based on allozyme electrophoresis (Georges & Adams, 1996), interbreeds freely with *E. m. macquarii* where they come into narrow contact in the Bulloo drainage (Georges, unpubl. data). Species status not warranted.

Distribution: Occupies the many permanent waterholes of the Cooper Creek drainage and lower reaches of the Diamantina; also in the Bulloo drainage.

— *Emydura macquarii krefftii* (Gray, 1871a) (Kreffts River Turtle)

1871 *Chelymys krefftii* Gray, 1871a, holotype, BMNH 1947.3.6.1, from Burnett River, Queensland, Australia. Synonymy of *Emydura krefftii* (junior) and *Emydura macquarii* follows that of Georges and Adams (1996).

1872 *Chelymys victoriae marmorata* Gray, 1872b, holotype, BMNH 71.9.25.5 (Stimson in pers. comm. with Cogger et al., 1983), from Burnett River, Queensland. Synonymy follows that of Wermuth and Mertens (1961) and Cogger et al. (1983).

1872 *Chelymys victoriae sulcata* Gray, 1872b, syntypes, BMNH 71.9.25.3–4 (Stimson in pers. comm. with Cogger et al., 1983), from Burnett River, Queensland. Synonymy follows Wermuth and Mertens (1961) and Cogger et al. (1983).

1889 *Emydura krefftii*—(Boulenger, 1889).

2003 *Emydura macquarii krefftii*—(Blackmore, 1969). First use of combination. (see also McCord et al., 2003).

A series of populations distinguished by the usual presence of a distinct post-ocular yellow stripe, which is uncommon (*E. m. nigra*, juveniles of *E. m. macquarii*) or rare (adult *E. m. macquarii*, *E. m. emmotti*) in the other subspecies. Distinguished also from *E. m. macquarii* on shell shape which is deeper and usually lacks posterior flaring. No morphological characters are consistently diagnostic, nor are they considered substantial enough to be used as species-defining characters. Allozyme data could not distinguish populations of *E. m. krefftii* from the other subspecies (Georges & Adams, 1996). Some mitochondrial haplotypes unique to some coastal populations are deeply divergent (Shaffer and Georges, unpubl. data). Species status not warranted.

Distribution: Occupies coastal rivers of Queensland from the Mary drainage in the south to the Normandy drainage in the north.

— *Emydura macquarii nigra* McCord et al., 2003 (Fraser Island Short-necked Turtle)

1985 *Tropicochelymys insularis* Wells & Wellington, 1985, *nomen nudum* following Iverson et al. (2001).

2003 *Emydura macquarii nigra* McCord et al., 2003, holotype, QM J48008, Lake MacKenzie, Fraser Island, Queensland (25°27'S, 153°04'E).

2004 *Emydura nigra*—Joseph-Ouni, 2003.

This subspecies occupies the oligotrophic acid dune lakes of Fraser Island and adjacent Cooloola Peninsula and are distinguished from the mainland forms largely by its melanism, small body size and associated ecological parameters. These may be local adaptation or phenotypic response to local conditions, and warrant further investigation. Degree of melanism, body size, facial markings (presence/absence of post-ocular stripe) and shell mottling vary from lake to lake. These lakes are isolated and have no history of connection with each other or the sea, and so the subspecies comprises an aggregation of populations showing some level of divergence and with a well defined geographic provenance. Not genetically distinct from other populations of *Emydura macquarii* based on allozyme electrophoresis (Georges & Adams, 1996). Species status not warranted.

Distribution: Occupies the many permanent dune lakes of Fraser Island and Lake Poona of Cooloola Peninsula on the adjacent mainland.

— *Emydura subglobosa* (Kreffft, 1876) (New Guinea Painted Turtle)

Species regarded as distinct from *Emydura victoriae* and the southern *Emydura* (*Emydura macquarii*) by virtue of its striking and characteristic colouration, and the leading and trailing spots on the iris.

This distinction was confirmed by allozyme electrophoresis (Georges & Adams, 1996), but its

distinction from *Emydura subglobosa worrelli* (Wells & Wellington, 1985) could not be confirmed genetically. The two were regarded as conspecific by Georges and Adams (1996), differing largely in colour (presence or absence of red suffusing of plastron and ventral soft parts), but the subspecific rankings have not been universally accepted. *Emydura subglobosa worrelli* has been regarded as a full species (Cann, 1998; Georges & Thomson, 2006). The two forms are retained as subspecies pending further detailed examination (see the *E. s. worrelli* subspecies account for further comment).

Key to subspecies

- 1 Ventral surfaces of shell and soft parts yellow, cream or grey, not suffused with red; facial stripe yellow, pink or bright salmon (fading or with darker blotches in older and macrocephalic individuals); macrocephaly common in adults *worrelli*
- Ventral surfaces of shell, head, neck, limbs and tail suffused with red; facial stripe bright yellow (fading in older individuals); macrocephaly absent *subglobosa*

— *Emydura subglobosa subglobosa* (Krefft, 1876) (New Guinea Painted Turtle)

- 1876 *Euchelymys subglobosa* Krefft, 1876, holotype, MCG CE2320, from Naiabui, on Amama River, SE Papua New Guinea.
- 1888 *Emydura albertisii* Boulenger, 1888, syntypes, MCG CE8430-1, from Mawatta, Binaturi River (as Katow), Papua New Guinea. Synonymy follows that of Cogger et al. (1983).
- 1888 *Emydura subglobosa*—Boulenger, 1888. First use of combination.
- 1985 *Tropicochelymys goodei* Wells & Wellington, 1985, *nomen nudum* following Iverson et al. (2001).
- 2003 *Emydura subglobosa subglobosa*—Artner, 2003. First use of combination.

A very distinctive and common form in southern New Guinea, distinguished by the bright red colouration of the plastron and ventral surfaces of the limbs, tail and neck.

Distribution: Southern New Guinea from but not including the Vogelkopf and Bomberi Peninsulas in the west to the Kemp-Welsh drainage in the east (Rhodin, 1993); Jardine River, Cape York Peninsula, Australia.

— *Emydura subglobosa worrelli* (Wells & Wellington, 1985) (Worrells Turtle or Diamond-head)

- 1985 *Tropicochelymys worrelli* Wells & Wellington, 1985, holotype, AMS R53689, from Caranbirini Waterhole, ca 21 km north of MacArthur River, Northern Territory, Australia (16°16'S, 136°05'E).
- 1985 *Tropicochelymys leichhardti* Wells & Wellington, 1985, *nomen nudum* following Iverson et al. (2001).
- 1998 *Emydura worrelli*—Cann, 1998.
- 2000 *Emydura subglobosa worrelli*—Georges & Adams, 1996; Georges et al., 2000. First use of combination.

This subspecies was first identified as a possible distinctive form by Cann (1972; 1978), then named by Wells and Wellington (1985) with inadequate description and scant diagnosis. Arguably a *nomen nudum*, but we follow Iverson et al. (2001) in accepting the name. The first adequate morphological description of the subspecies was provided by Cann (1998). Allozyme comparisons did not reveal differences significant enough to warrant its recognition as a species separate from *E. subglobosa* (Georges & Adams, 1992; 1996). However, the two subspecies occupy very different habitats, differ consistently in colour, and large adults of *E. s. worrelli* are commonly macrocephalic, whereas those of *E. s. subglobosa* are never so. The two subspecies of *Emydura subglobosa* may be full species, subject to confirmation by future detailed morphological and genetic comparisons.

Distribution: Upland reaches of the rivers draining the Arnhem Land Plateau, Northern Territory, Australia (western extent, Daly drainage), major rivers draining into the Gulf of Carpentaria, from the Roper drainage in the west, east to the Gregory-Nicholson drainage of Queensland.

Emydura tanybaraga Cann, 1997d (Northern Yellow-faced Turtle)

- 1997 *Emydura tanybaraga* Cann, 1997d, holotype, AMS R125498, from Policemans Crossing, Daly River, Northern Territory, Australia (13°46'S, 130°43'E).
- 2008 *Emydura subglobosa tanybaraga*—Artner, 2008.

Status uncertain. Established as a species by one fixed allelic difference from *Emydura victoriae* in microsympatry in the Daly River (at Policemans Crossing) and one fixed difference from *Emydura subglobosa worrelli* (from Sleisbeck) in sympatry (Georges & Adams, 1996). This weak level of genetic divergence is common across all comparisons among species of *Emydura*, and suggests recent radiation of the genus. Morphological characters to diagnose *E. tanybaraga* from *E. victoriae* are substantial (refer to the key above), but less so between *E. tanybaraga* and *E. subglobosa worrelli*. The latter two species are very difficult to distinguish consistently in the field, and further examination of their status using a combination of DNA sequence data and morphological data is warranted. No subspecies are recognised.

Distribution: Lowland reaches of the Finnis-Reynolds, Daly, Alligator Rivers drainages of the Northern Territory, Australia, and the rivers flowing to the east (Stewart River) and west (e.g. Mitchell River) on Cape York Peninsula. Presence in intervening rivers not well established. Unlikely to extend as far north as the Jardine River, Cape York.

***Emydura victoriae* Gray, 1842 (Northern Red-faced Turtle)**

1842 *Hydraspis victoriae* Gray, syntypes (2), BMNH 1947.3.5.95–96, from Victoria River, NT, Australia.

1964 *Emydura victoriae*—Worrell, 1963. First use of combination.

Species of *Emydura* from northern Australia have commonly been confused, with some authors recognizing only one species (erroneously *Emydura australis*, Worrell, 1970; Ernst & Barbour, 1989), others making the distinction on the basis of colouration (red-faced or yellow faced), with the red-faced and yellow-faced forms variously called *E. australis* and *E. victoriae*, respectively (Cogger, 1975; Cann, 1978) or the reverse (Cogger, 2000). Clarification occurred with the publication of the *Zoological Catalogue of Australia I: Amphibia and Reptilia* (Cogger et al., 1983) which removed *E. australis* from consideration, treating it as a junior synonym for *E. macquarii* citing type locality clarification by Gray (1872b). Georges and Adams (1992; 1996) demonstrated that the northern taxa were represented by three species, sympatric in the Daly River drainage, which have subsequently been assigned to *E. victoriae* (Gray, 1842) (Northern Red-faced Turtle), *E. tanybaraga* Cann, 1997d (Northern Yellow-faced Turtle) and *E. subglobosa worrelli* (Wells & Wellington, 1985) (Diamond-head Turtle).

Some confusion remains with populations of *E. victoriae* from the Kimberley region of Western Australia assigned to *E. australis* (Tucker et al., 2005; Tkach & Snyder, 2008), despite Gray's assignment of the holotype of the latter to the Macquarie River in New South Wales (Gray, 1872b). Some authors erroneously restricted the name *E. australis* to the diminutive forms found in the King Edward and Prince Regent Rivers of the Kimberley region (Cann, 1998:167–68).

In this account, we treat the *Emydura* of northern Australia with triturating surfaces of the maxillary sheath expanded to meet medially as a crushing plate on the roof of the mouth, a bright red pre-ocular stripe (when present), iris an unbroken ring without leading and trailing dark spots, as *E. victoriae*. This species under this definition includes populations extending across the Kimberley region of Western Australia to the Fitzroy drainage in the west, until evidence is presented to indicate otherwise. No subspecies are recognised.

Genus *Myuchelys* Thomson & Georges, 2009 (Australasian Helmeted Turtles)

2009 *Myuchelys latisternum* (Gray, 1867), type species by original designation.

Turtles of moderate size that primarily inhabit tributaries and headwaters of rivers throughout their range; head and neck, when extended, much shorter than the carapace; gular scutes entirely separated by the intergular scute; no alveolar ridge on the triturating surfaces of the jaw sheaths; cervical scute present (except as a rare variant) in most species; a horny casque (head shield) on top of the head of adults, entire, with a prominent well-defined process extending down the parietal ridge toward the tympanum; temporal region covered with prominent scales; temporal stripes absent; eye with a distinct iris; front feet with five claws, rear with four claws.

Refer to the taxonomic account for the genus *Eelseya* presented above for background on the establishment of this genus. Diagnosis is on the basis of shared primitive characters only, with no morphological synapomorphy identified to unite the four species (Thomson & Georges, 2009), relying rather on synapomorphies derived from molecular data (Georges & Adams, 1992; Georges et al., 1998). The

relationships of a fifth species, *Myuchelys novaeguineae*, are uncertain. The allozyme data of Georges and Adams (1992) place it between the Queensland and Northern clades of *Elseya* (sensu stricto) but this requires more detailed examination as a number of morphological features place it with *Myuchelys*.

Key to species

- 1 Carapace free of regular, distinct dark spots; cervical scute present or absent; Australia..... 2
 - Distinct dark spot on each vertebral scute and each costal scute retained into adulthood; plastron cream or grey with darker markings but not distinct streaks; cervical scute present (except as a rare variant); New Guinea *novaeguineae*
- 2 Carapace broadly oval, expanded posteriorly, with a serrated hind edge in adults, except in very old individuals; dorsum of neck with prominent pointed tubercles 3
 - Carapace broadly oval, not expanded posteriorly, with a smooth outline in adults; dorsum of neck with low rounded tubercles 4
- 3 Cervical scute absent (except as a rare variant); iris with a leading and a trailing dark spot; coastal northern New South Wales, Queensland, Northern Territory *latisternum*
 - Cervical scute present (except as a rare variant); iris clear, lacking a leading and a trailing dark spot; north-eastern headwaters of the Murray-Darling basin, west of the Great Dividing Range..... *bellii*
- 4 Undersurface of shell and soft parts typically with bright yellow colouration, except in very old individuals; tail with a ventral yellow stripe from anal notch to the cloaca; lateral precloacal continuous or broken yellow stripes meet the central stripe at the cloaca; undersurface of the tip of the tail yellow; Manning River, New South Wales..... *purvisi*
 - Undersurface of shell and soft parts not brightly coloured except in very young individuals; tail without bright markings; Bellinger River, New South Wales..... *georgesii*

Myuchelys bellii (Gray, 1844) (Western Sawshelled Turtle)

- 1844 *Phrynops bellii* Gray, 1844, holotype OUM 8460, type locality not designated.
 1998 *Elseya bellii*—Cann, 1998.
 2008 *Elseya latisternum bellii*—Artner, 2008.
 2009 *Myuchelys bellii* — Thomson & Georges, 2009. First use of combination.

This species occupies the Namoi and Gwydir sub-drainages of the Murray-Darling basin, above the escarpment of the New England Tableland, and was established as a distinct biological species on detecting fixed allelic differences from its nearest relative, *Myuchelys latisternum*, with which it is in broad parapatry (Georges & Adams, 1992). Cann (1998:209–213) subsequently presented morphological data to assign populations of the Namoi-Gwydir to *Phrynops bellii* which, on examination of the holotype, is clearly a member of *Myuchelys* from Australia. However, genetic confirmation of the provenance of the holotype is needed. Cann regards the populations since found in Bald Rock Creek of the adjacent Border Rivers sub-drainage as a separate species (Cann, 1998:214–216), but failed to name it. Recent examination of genetic divergence between the Bald Rock Creek populations and those of the adjacent Namoi and Gwydir sub-drainages found only minor differences (Fielder, unpubl. data), and in the absence of morphological data and satisfactory analysis to the contrary, we regard these populations as a single species. No subspecies are recognised.

Distribution: Murray-Darling Drainage: Namoi and Gwydir drainages of the New England Tableland, New South Wales and the headwaters of the Border Rivers drainage of northern New South Wales and southern Queensland, Australia.

Myuchelys georgesii (Cann, 1997a) (Georges Helmeted Turtle)

- 1997 *Elseya georgesii* Cann, 1997a, holotype, AMS R31721, from Bellinger River 30°25'S, 152°46'E.
 2008 *Elseya latisternum georgesii*—Artner, 2008.
 2009 *Myuchelys georgesii*—(Thomson & Georges, 2009). First use of combination.

Populations of this species from the Bellinger River, together with the broadly similar Manning River form, were known to be distinctive long before the descriptions appeared (Cann, 1978; Legler, 1981). The Bellinger River form was established as distinct from the Manning River form on detecting 20% fixed allelic differences in allopatry (Georges & Adams, 1996). Subsequently named and adequately described

in the magazine *Monitor* (Cann, 1997a), not subject to peer review; the article later reproduced in a more widely available book (Cann, 1998). No subspecies are recognised.

Distribution: Restricted to the Bellinger River drainage of north coastal New South Wales, Australia.

***Myuchelys latisternum* (Gray, 1867) (Common Sawshell Turtle)**

1867 *Elseya latisternum* Gray, 1867, holotype, BMNH 1947.3.4.13, from North Australia.

1871 *Euchelymys spinosa* Gray, 1871b, holotype, BMNH 1946.1.22.77, from North Australia. Synonymy follows that of Gray (1872a) and Boulenger (1889).

2009 *Myuchelys latisternum*—Thomson & Georges, 2009. First use of combination.

An exceptionally widespread species, polytypic, may be a species complex. An evaluation across its range using allozymes found two fixed allelic differences between the populations of the Arnhem Land Plateau of the Northern Territory and those of the Richmond of New South Wales¹¹, but the differences were not sustained beyond clinal variation when intermediate populations were considered (Georges & Adams, 1996). Distinct genetically from other members of *Myuchelys* (Georges & Adams, 1992). No subspecies are recognised.

Distribution: From the Richmond drainage of north coastal New South Wales to the Jardine at the tip of Cape York, across the rivers draining into the Gulf of Carpentaria, east to the rivers draining the Arnhem Land Plateau. The Daly and Mary drainages, Northern Territory, mark the western extent to its distribution. Occupies principally headwaters and tributaries.

***Myuchelys novaeguineae* (Meyer, 1874) (New Guinea Spotted Turtle)**

1874 *Platemys novaeguineae* Meyer, 1874, holotype, MTD 8222, from Passim, NW New Guinea.

1888 *Emydura novaeguineae*—Boulenger, 1888.

1911 *Emydura schultzei* Vogt, 1911, holotype, ZMB 22182, from river west of the Tami Mouth, New Guinea. Synonymy follows that of Goode (1967) and Wermuth and Mertens (1977).

1967 *Elseya novaeguineae*—Goode, 1967.

1969 *Elseya latisternum novaeguineae*—Blackmore, 1969.

1985 *Elseya dentata novaeguineae*—Obst, 1985.

2009 *Myuchelys noveguineae*—Thomson & Georges, 2009. First use of combination.

A species of uncertain affinities, passed variously between the genera *Elseya* and *Emydura* (Boulenger, 1889; Goode, 1967). Allozyme data place it in *Elseya*, nested between the Queensland and Northern clades (Georges & Adams, 1992); Boulenger (1889) regarded its affinities to lie with *Myuchelys latisternum*. We have tentatively placed it in *Myuchelys*, pending more detailed DNA sequence analyses. Possibly a species complex (Rhodin & Genorupa, 2000). Species has four distinct mitochondrial haplotype clades which distinguish groups of populations along conventional biogeographic lines (Georges and McCord, unpubl. data), but none are regarded by us as sufficiently distinct to warrant recognition at species or subspecies level. Artner (2008) refers to the northern New Guinea form as a distinct subspecies, *Elseya novaeguineae schultzei*.

Distribution: New Guinea and associated islands.

***Myuchelys purvisi* (Wells & Wellington, 1985) (Manning River Helmeted Turtle)**

1985 *Elseya purvisi* Wells & Wellington, 1985, holotype, AMS R44654, from a river [Manning River] 15 km S., 32.3 km E. of Nowendoc, New South Wales (31°39'S, 152°04'E).

2008 *Elseya latisternum purvisi*—(Artner, 2008).

2009 *Myuchelys purvisi*—Thomson & Georges, 2009. First use of combination.

Named by Wells and Wellington (1985) with inadequate description and scant (and erroneous) diagnosis (Iverson et al., 2001). Established as a distinct species based on genetic comparisons, in allopatry (Georges & Adams, 1996). Adequately described for the first time by Cann (1998). Neural bones present as surface elements of the carapace (absent in *M. georgesi*) (Thomson & Georges, 1996). External

11. The south east Queensland populations of *Myuchelys latisternum* have been named by Wells (2009) as *Wollumbinia dorsii*, but the account appears in a privately prepared and circulated document that does not, in the opinion of the authors, meet the provisions of ICZN Articles 8 and 9 and Recommendation 8D and so is not considered a publication for the purposes of nomenclature. In any case there is no evidence to suggest that they warrant separate recognition at the level of species.

morphology very similar to that of *M. georgesi*, from which differs largely in intensity of colouration. No subspecies are recognised.

Distribution: Restricted to the Manning River drainage of coastal New South Wales, Australia.

Genus *Pseudemydura* Siebenrock, 1901

1901 *Pseudemydura umbrina* Siebenrock, 1901, type species by monotypy.

A genus represented by a single living species *Pseudemydura umbrina* Siebenrock, 1901 restricted to two very small sites in the Swan River drainage, near Perth, Western Australia. Short neck, head and neck, when extended, much shorter than the carapace; Carapace squarish in outline, not much longer than wide; vertebral scutes all wider than they are long; posterior marginal scutes elevated over the tail; margin of carapace smooth; gular scutes entirely separated by the intergular scute, the latter partially separating the pectoral scutes; triturating surfaces of the jaw sheaths lacking a prominent alveolar ridge; cervical scute present, recessed behind the anterior extent of the first and second marginal scutes; robust head with a horny casque (head shield); temporal region smooth; large tubercles on the dorsal surface of the neck; no temporal stripe; iris distinct; front feet with five claws, rear with four claws.

***Pseudemydura umbrina* Siebenrock, 1901 (Western Swamp Turtle)**

1901 *Pseudemydura umbrina* Siebenrock, 1901, holotype, NHMW 89 (8450) =1296, from Australia.

1954 *Emydura inspectata* Glauert, 1954a, holotype, WAM R11092, from Warbrook, ca 24 miles N of Perth, Western Australia. Synonymy follows that of Glauert (1954b).

Uncontroversial. Original description adequate to establish status as a distinct species. Genetic evaluation has not been undertaken. Affinities unclear. No subspecies are recognized.

Distribution: Restricted to the ephemeral swamps in the Swan drainage, near Perth, Western Australia.

Genus *Rheodytes* Legler & Cann, 1980

1980 *Rheodytes leukops* Legler & Cann, 1980, type species by monotypy.

A genus represented by a single living species *Rheodytes leukops* Legler & Cann, 1980 restricted to the Fitzroy drainage of eastern Queensland, Australia. Moderately long neck, head and neck, when extended, much shorter than the carapace; margin of carapace smooth in adults, serrated in juveniles; suture between the second and third costal scutes contacting the sixth marginal scute, that between the third and fourth costal scutes contacting the eighth marginal scute (rib tips of costals 2–4 articulate with peripherals 4–6); gular scutes entirely separated by the intergular scute; triturating surfaces of the jaw sheaths lacking a prominent alveolar ridge; cervical scute present (except as a rare variant); head with a horny casque (head shield); temporal region covered with prominent raised tubercles; large conical tubercles on the dorsal surface of the neck; no temporal stripe; iris distinct with a characteristic white ring; huge cloacal bursae; front feet with five claws, rear with four claws.

***Rheodytes leukops* Legler & Cann, 1980 (Fitzroy River Turtle or White-eyed River Diver)**

1980 *Rheodytes leukops* Legler & Cann, 1980, holotype, QM J31701, from Fitzroy River, 63 km N and 25 km E of Duaringa, Queensland, Australia (23°09'S, 149°55'E).

Uncontroversial. Original description adequate to establish status as a distinct species. Genetically very distinct, affinities unclear (Georges & Adams, 1992; 1996). No subspecies are recognized.

Distribution: Restricted to the Fitzroy drainage of central coastal Queensland, Australia.

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