

**Diagnosis of Living and Fossil Short-necked Turtles of the Genus
Elseya using skeletal morphology**

by

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A thesis submitted in fulfilment of the requirements of the Degree of Masters of Applied Science at the University of Canberra.

January 2015

Certificate of Authorship of Thesis

Except where clearly acknowledged in the statement of contribution, footnotes, quotations and the bibliography, I certify that I am the sole author of the thesis submitted today entitled – Diagnosis of the Living and Fossil Short-necked Turtles of the Genus *Elseya* using skeletal morphology.

I further certify that to the best of my knowledge the thesis contains no material previously published or written by another person except where due reference is made in the text of the thesis.

The material in the thesis has not been the basis of an award of any other degree or diploma except where due reference is made in the text of the thesis.

The thesis complies with University requirements for a thesis as set out in Gold Book Part 7: Examination of Higher Degree by Research Theses Policy, Schedule Two (S2).

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Date:

Statement of Contribution

As is the modern trend, a substantial proportion of this thesis has been published or submitted for publication. These papers, which also form the chapters of this thesis, have multiple authors. The following is a statement of contribution to these chapters by me and the other authors.

CHAPTER 2: Thomson, S. & Georges, A. 1996. Neural bones in Australian chelid turtles. *Chelonian Conservation and Biology* 2(1), 82-86

The work contributing to this paper was undertaken by me under the supervision of Dr Arthur Georges who provided advice and guidance on the initial decision to proceed with the work, the design of the study, the science leading to the outcome and the preparation of the publication. The contribution of Arthur Georges, although contributing intellectually, did not exceed that which would be expected of an academic supervisor.

CHAPTER 3: Thomson, S.A., White, A., & Georges, A. 1997. Re-evaluation of *Emydura lavarackorum*: identification of a living fossil. *Memoirs of the Queensland Museum* 42:327–336.

The work contributing to this paper was undertaken by me under the supervision of Dr Arthur Georges who provided advice and guidance on the initial decision to proceed with the work, the design of the study, the science leading to the outcome and the preparation of the publication. Dr Arthur White was the scientist who first described the species reassigned in this paper, and it was only appropriate to provide him the opportunity to discuss the reinterpretation. Arthur White engaged in discussions with me on the basis of reassignment of the fossils and the relevance of the fossils which helped me formulate my ideas. The contribution of Arthur Georges, although contributing intellectually, did not exceed that which would be expected of an academic supervisor.

CHAPTER 4: Thomson, S.A. & Mackness, B. 1999. Fossil turtles from the early Pliocene Bluff Downs Local Fauna, with a description of a new species of *Elseya*. *Transactions of the Royal Society of South Australia* 123:101–105.

The work contributing to this paper was undertaken by me under the supervision of Dr Arthur Georges who provided advice and guidance on the initial decision to proceed with the work, the design of the study, the science leading to the outcome and the preparation

of the publication. At the time, the late Brian Mackness was the principal paleontologist at the Bluff Downs fossil site. He gave me access to the fossils described in the paper and stratigraphic data on the age of the fossils. The contribution of Arthur Georges, although contributing intellectually, did not exceed that which would be expected of an academic supervisor.

CHAPTER 5: Thomson, S.A. 2000. A revision of the fossil chelid turtles (Pleurodira) described by C.W. DeVis (1897). *Memoirs of the Queensland Museum* 43:593–598.

The work contributing to this paper was undertaken by me under the supervision of Dr Arthur Georges who provided advice and guidance on the initial decision to proceed with the work and the preparation of the publication. I am the sole author on this publication, reflecting that the contribution of Arthur Georges and others as acknowledged, was not sufficient to warrant co-authorship.

CHAPTER 6: Thomson, S., Georges, A. & Limpus, C. 2006. A New Species of Freshwater Turtle in the Genus *Elseya* (Testudines: Chelidae) from Central Coastal Queensland, Australia. *Chelonian Conservation and Biology*. 5: 74-86.

The work contributing to this paper was undertaken by me under the supervision of Dr Arthur Georges who provided advice and guidance on the initial decision to proceed with the work, discussed with me his prior molecular work which complemented my morphological work, discussed the science leading to the outcome and assisted with the preparation of the publication. Dr Colin Limpus and Arthur Georges provided the ecological data included in the paper, and provided text for that part of the paper. Apart from that, the contribution of Arthur Georges, although contributing intellectually, did not exceed that which would be expected of an academic supervisor.

CHAPTER 7: Thomson, S. and Georges, A. 2009. *Myuchelys* gen. nov.— a new genus for *Elseya latisternum* and related forms of Australian freshwater turtle (Testudines: Pleurodira: Chelidae). *Zootaxa* 2053:32–42.

The work contributing to this paper was undertaken by me under the supervision of Dr Arthur Georges who provided advice and guidance on the initial decision to proceed with the work, discussed with me his prior molecular work which complemented my morphological work and assisted with the preparation of the publication. The

contribution of Arthur Georges, although contributing intellectually, did not exceed that which would be expected of an academic supervisor.

Anders Rhodin, Russ Mittermeier, Peter Pritchard, Uwe Fritz and Roger Bour provided comment and suggestions on the various chapters provided to them as late draft manuscripts.

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Signature of Candidate

Acknowledgements

I thank the many institutions and their curators who kindly supplied specimens used in this study and who provided advice on the many taxonomic side issues that arose during this work. They include Ross Sadler (Australian Museum), Patrick Couper (Queensland Museum), Paul Horner (Northern Territory Museum), Laurie Smith (Western Australian Museum), the late John Legler (University of Utah), Peter Pritchard (Chelonian Research Institute), John Wombey (Australian National Wildlife Collection), Jose Rosado (Museum of Comparative Zoology) and Colin MacCarthy (Natural History Museum).

I also thank the many individuals who assisted with access to particular specimens and provided other assistance over the years, including Uwe Fritz (Senckenberg Dresden, Königsbrücker Landstr.), Gerald Kuchling (University of Western Australia), Roger Bour (Muséum National d'Histoire Naturelle, Paris), John Cann (Sydney), Bill McCord (New York), Mike Archer (University of New South Wales), Arthur White (Sydney) and Rod Kennett (Canberra).

The chapters of this thesis have been published and I wish to thank the various people who co-authored those publications, including Arthur Georges, the late Brian Mackness, Arthur White and Colin Limpus. I also thank those who reviewed those chapters, including Anders Rhodin, Russ Mittermeier, Peter Pritchard, Uwe Fritz and Roger Bour. Also thanks go to Reiner Rehwinkle, Simone Reynolds, Peter Ogilvie and Mike Palmer-Allen for technical support in various parts of this work.

Owing to the circumstances that led to the delays in completing this thesis, I also acknowledge Ross Thompson and others who gave me the opportunity to finish and submit it toward a degree with Masters. Without the opportunities given me and the encouragement of Hussam Zaher (Museu de Zoologia da Universidade de São Paulo) and Arthur Georges, I could not have finished this.

I also thank Arthur Georges for supervising my thesis work, and to Steve Sarre for agreeing to co-supervise the completion of this work after my original second supervisor, Will Osborne, had retired.

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Chapter 1: Introduction

The taxonomy and systematics of any group of species is a foundation for understanding the world's biodiversity, along with ecology (Kim and Byrne, 2006). The recent domination of the earth by a single species, humans, has led to the view that major and potentially critical changes to biodiversity are upon us (Dobson, 2005). The current crisis in biodiversity worldwide is often referred to as the Sixth Extinction (Mittermeier et al., 2000). Full appreciation of the biodiversity crisis requires a thorough assessment of the number of species on our planet, as a necessary though not entirely sufficient (Adams et al., 2014) contribution to knowledge. The identification of species, the relationships among them, and an agreed nomenclature are all elements of such an assessment. These key elements are used in all fields of biological science.

Turtles are ancient lineages of vertebrates with a relatively small number of extant species, approximately 453 taxa (van Dijk et al., 2014). However they have a disproportionate number of endangered species, with 10% of species considered to be threatened (Buhlman et al., 2009), an estimate rising to 60% considered either threatened or already extinct in 2014 (van Dijk et al., 2014). With this level of predicted decline and extinction, it is important to determine current species richness and diversity, and identify hotspots for conservation efforts (Buhlmann et al., 2009). The first step in this process is to identify and name the species in each region, notwithstanding the recent development of other techniques such as DNA barcoding of composite samples (Hebert and Gregory, 2005; Smith et al. 2005) as an index to biodiversity.

Unfortunately, many studies of biodiversity patterns lack taxonomic rigor and precision owing to flawed taxonomic concepts and poor quantification at or below the level of species (Bertrand et al., 2006). A disturbing contributor to this deficiency is the declining numbers of qualified taxonomists, despite their crucial role documenting biodiversity in a time of crisis, in the context of only less than 20% of the species on Earth adequately described (Kim and Byrne, 2006). Without a stable nomenclature and a well-defined taxonomy, errors will occur in the ensuing studies of ecology and the application of ecological knowledge to management (Thomson, 1997; Bortolus, 2008). A case in point, only recently published, clearly demonstrates the importance of having the taxonomy and nomenclature correct. Four horticultural pest tephritid fruit fly species have been recognized and managed separately but they were almost identical, both genetically and morphologically, to the Oriental fruit fly *Bactrocera dorsalis* (Schutz et al. 2014). Diagnosis of these species was problematic, yet crucial because of the economic importance and trade implications of these

species in regards to plant protection and food security (Schutz et al. 2014). An integrated multidisciplinary effort showed that the five species that were difficult if not impossible to diagnose, were indeed two species, *Bactrocera carambolae* and *Bactrocera dorsalis*, with re-descriptions and diagnostic characters now available. This had important flow-on implications for pest management, quarantine, international trade, postharvest treatment and basic research on these pest species previously confounded by poor taxonomy (Schutz et al. 2014).

In a second example, Groves (2014) discussed the impact of over-lumping on scientific understanding. Ohwaki et al. (1974) studied microbial fermentation in the species that they designated as *Colobus polykomos* (*sensu* Schwarz, 1929), only to later find they were working with *Colobus guereza*. These two species occur in different parts of Africa and have differing diets (Groves, 2014) with obvious implications for studies of gut microbial composition. Groves (2014) applied the Phylogenetic Species Concept, a modification of the Evolutionary Species Concept (Wiley, 1978) to generate a classification that is defined on clear diagnosability (Groves, 2014) and so likely to avoid such confusion in future.

To demonstrate the costs of inadequate taxonomy, the case of *Salvinia molesta* is noteworthy, in that it is controlled in a number of countries biologically by introducing the weevil *Cyrtobagous salviniae* also from South America. Its control rested upon not only on the correct identification of the species invading Australian waters, but also on the race of beetle occupying that species as host in its natural range (Room et al., 1981). Similarly, timely identification of the outbreaks in Thailand as *Salvinia cucullata* avoided mistargeted management and hence the probable waste of \$5 million budgeted to eradicate the weed in Thailand. The proposal to introduce *Cyrtobagous salviniae*, likely to be ineffective, was subsequently withdrawn (Smith et al. 2011).

In two final cases, more relevant to the subject material of this thesis, cloacal breathing was reported in *Myuchelys georgesi*, at the time an undescribed form known to be a distinct species (Georges and Adams, 1992), but under the name “*Elseya latisternum*” (King and Heatwole, 1994). This led subsequent workers investigating new instances of this trait to leave *Myuchelys latisternum* out of their studies, the work having already been done. It had not been done, the use of the nearest named species for the then undescribed but distinct taxon *Myuchelys georgesi*, having misled them. In a second case, *Emydura macquarii* from the Bellingen River was regarded as a distinct taxon by Cann (Cann, 1977; 1998) on the basis of morphological analysis that was unpublished or published without the benefit of peer review. Application of the precautionary principle in the face of limited information and low capture rates (Cann 1998; Spencer & Thompson 2000) resulted in this taxon being classified as

Vulnerable and being listed in the Action Plan for Australian Reptiles (Cogger et al. 1993), and later the NSW list of threatened species and the national EPBC Act, with consequent management implications (Thomson, 1997). Community engagement in riparian restoration projects and fox control programs rested upon saving this local iconic species. When the requisite science was belatedly done, it showed that this “species” was an unremarkable population of *Emydura macquarii*, in all likelihood introduced (Georges et al. 2007), and perhaps hybridizing with and threatening the true endemic *Myuchelys georgesi*. This is a clear case where not understanding the taxonomy of the population potentially wasted efforts and funding earmarked for vulnerable species (Thomson, 1997; Georges et al. 2007). Management funding is finite, so conservation often is governed by decisions on priorities, which in turn are governed in part by taxonomy and phylogenetic distinctiveness. For this reason, it is important to understand the species geographical and taxonomic boundaries (Thomson, 1997). The Bellinger population of *Emydura macquarii* lost its Vulnerable status in NSW in 2009 and was withdrawn from the list of threatened species governed by the EPBC Act.

The species is the basic unit of our current nomenclatural system and the only one that is considered to represent a real natural entity, as against the higher orders which are constructs for purposes of nomenclature. It is important to realize that there is a difference between species delimitation and species concepts (de Queiroz, 2007). A further issue has been the changing face of this concept with many ideas on what a species is being incompatible with other ideas (de Queiroz, 2007). With as many as 24 such concepts reviewed by Mayden (1997) this has presented a major issue in developing taxonomy for various groups. In an attempt at a Unified Species Concept, de Queiroz (2007) showed that all the available concepts had a common element, that is, that species are separately evolving metapopulation elements. He goes on to state that this attribute is a necessary and sufficient component of a definition of species, with all other attributes discussed in the literature being recognized but unnecessary. Thus in identifying the commonality, and arguing that this commonality is both necessary and sufficient in a species concept, de Queiroz believes his concept resolves the issues that have been the subject of heated debate in recent years. Nevertheless, because the Unified Species Concept does not distinguish between metapopulations on independent trajectories because of geographical happenstance from those isolated from gene flow because of reproductive barriers likely to be sustained if the “species” come back into sympatry, his concept has not achieved universal acceptance. In an operational sense, a universal species concept for metazoans remains elusive and may not be

possible (Hey, 2001). The consequence is that opinions and decisions on the species that comprise a fauna still 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. In this thesis, I adopt the concept of species outlined in the paper by Georges and Thomson (2010) when dealing with extant forms. Briefly, 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 Diagnosable Terminal Taxon or Operational Taxonomic Unit is an aggregation of extant populations that are the descendants of a lineage and which have diverged to the point of accumulating one or more diagnostic characters (all individuals can be assigned unambiguously). It could be a deme, or a geographically isolated population of a species, but even though it is diagnosable, it is not regarded as a species.

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). Again, ESUs, even though they may be diagnosable and occupy a discrete geographical range (in allopatry), are not regarded as species. This contrasts with the alternate view that is often taken (e.g. Fujita et al., 2012).

Broadly, I 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 when they come to be 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 (usually in sympatry), subjectively on magnitude of difference otherwise (allopatry).

The genus is historically seen to be a natural entity, that is, defined to be consistent with phylogeny, along with other higher taxa (Simpson, 1953, Mayr, 1942). By the middle of the 20th century, it was seen to be a natural group that took into account the process of its formation and was also discrete (Humphreys & Barraclough, 2014). At the present time genera, are considered to be human constructs both conceptually and operationally (Georges and Thomson, 2010), that are useful in conveying information about similarity of the species within them and their collective differences from other genera of species (Clayton, 1983). They are objective in the sense that they are required to contain only monophyletic assemblages of species, but subjective in the sense that they carry more information on phenetic difference and similarity than conveyed solely by phylogeny (Georges and Thomson, 2010). These two considerations govern which clades within a phylogeny are regarded as genera. With the more recent heavy usage of phylogenetics, particularly in molecular work, the focus has shifted to clades with little consideration for the processes involved (Humphreys & Linder 2009). It is considered that there are no shared processes above the level of species that would form an Evolutionary Significant Unit (ESU), however, recent modelling using mammals as a test group would indicate this is not true (Humphreys & Barraclough, 2014).

The major defining factor for genera, or indeed any higher level category, is monophyly. Hence, when a genus is shown to be paraphyletic, a decision is required to split into smaller genera or to combine with other genera, until a monophyly is achieved. New genera may be erected under other circumstances. The genus also serves to convey similarity and collective difference, so can be used to define in addition to monophyly for a group of species that share similarities but that are separated from other such groups of species by a decided gap (Mayr, 1969). 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).

Species concepts, and perhaps also the concept of genus, that apply to extant forms do not apply to fossil forms. It is difficult to define the concepts of reproductive isolation for fossils in any operational sense, and similar difficulties present in defining the process of speciation. These concepts, when applied to fossils, are essentially typological; only rarely are we able to examine fossils in the context of closely related extant forms. However, the scope of taxonomy does apply to determining relationships between living and fossil taxa, allowing

us to see species through time. In recent years, we have seen the development of methods for calibrating molecular phylogenies, using well-defined fossil taxa whose relationships have been determined through apomorphy (Parham et al, 2012). When fossils are used to calibrate molecular data, it is crucial that the age and phylogenetic position of the fossil is known (Parham, 2012). As such, in their recent work on this concept Parham et al (2012), proposed five requirements for a fossil to be of value for dating molecular trees. These include an apomorphy-based phylogeny, identification of type and justification for additional specimens, age and locality and reconciliation of morphological and molecular data. However, in order to achieve this goal it is also necessary to have well defined living taxa that are morphologically diagnosed using apomorphy. Lack of morphological diagnosis of the living species and genera of turtles in the family Chelidae has greatly impeded progress, and this is the reason d'etre for this thesis work.

In Australia the freshwater turtle fauna is dominated by a single family, the Chelidae, with only one native species, *Carettochelys insculpta*, not belonging to this family (Georges, 1994). Recent analysis places the Australasian region as having one of the highest diversities of turtles with approximately 40 species (van Dijk et al., 2014), not including sea turtles. Australasia's turtle fauna is also highly endemic with all freshwater species in Australia and almost all from New Guinea found nowhere outside this region (Bulhman et al., 2009; van Dijk et al, 2014).

The turtles of the genus *Elseya*, Gray 1867 (Pleurodira: Chelidae), the primary subject of this thesis, have had a long and complicated history. Originally described in 1867 by John Edward Gray the genus was erected for the species *Elseya dentata* (Gray, 1863) and *Elseya latisternum* (Gray, 1867). The type species is *Elseya dentata* by subsequent designation (Lindholm, 1929). The type locality of the type species is Beagle's Valley on the Upper Victoria River in the Northern Territory (Gray, 1863). The genus initially was characterized by a horny shield on the dorsal surface of the head, flat polygonal plates on the temples, cheeks and throat, prominent tubercles on the dorsal surface of the neck, a pair of tubercles on the chin and the usual absence of a cervical scute (Gray, 1867, 1872).

Boulenger (1889) redefined the genus as having an alveolar ridge, a longitudinal ridge on the maxillary triturating surface, present only in *Elseya dentata*. *Elseya latisternum* and *Elseya novaeguineae* were placed in the genus *Emydura*. Subsequently, Goode (1967) expressed little faith in the alveolar ridge as a taxonomic feature at the level of genus, citing cases of variation in this feature among species of well recognized cryptodiran turtle genera and transferred *Elseya latisternum* and *Elseya novaeguineae* back to *Elseya*.

Since Goode's rejection of the importance of the alveolar ridge there has been considerable argument as to the validity of the genus *Elseya*. Gaffney (1977) was unable to differentiate the two genera consistently using cranial characters and Frair (1980) could not differentiate them using total serum protein electrophoresis. Species within the two genera have indistinguishable karyotypes (Bull and Legler, 1980), and the level of divergence of *Elseya* and *Emydura* in serological comparisons is comparable only to that of species groups within the *Chelodina* (Burbidge et al., 1974). Gaffney (1979) included the *Elseya* in *Emydura* and Frair (1980) suggested on the basis of his studies that *Elseya novaeguineae*, *Elseya latisternum*, *Emydura macquarii* (as *Emydura signata*) and *Emydura subglobosa* should be placed in the same genus. McDowell (1983) interpreted a wide range of morphological characters as indicating that the closest relative of *Elseya dentata* is *Emydura victoriae* (as *Emydura australis* (including *Emydura macquarii* (as *Emydura krefftii*) and *Emydura subglobosa*) and not *Elseya latisternum*. He concluded that the generic recognition of *Elseya* is unwarranted, and synonymized *Elseya* with *Emydura*.

A contrary interpretation to that of McDowell (1983) follows confirmation by electrophoretic evidence that the genus *Elseya* is paraphyletic, comprising two distinct clades. The closest common ancestor of the species of *Elseya* has the species of *Emydura*, and possibly *Elusor* and *Rheodytes*, among its descendants (Georges and Adams, 1992). Georges and Adams regarded the lumping of these taxa into a single genus resulted in too great a loss of information (genus conveys both similarity and collective difference) and recommended to split the genus *Elseya* (now *Elseya* and *Myuchelys*) and retain *Emydura*. It was at this point in the history of the genus *Elseya* that the work presented in this thesis began.

The broad aim of my thesis is to delimit and diagnose species of the genus *Elseya*, a genus once thought to only have a few widely distributed species, including resolving of the reported parphyly with respect to *Emydura* (Legler, 1981; Georges and Adams, 1992). More specifically, my objectives were to identify and describe characters that can be used as apomorphies to define the relationships between the species and genera; to diagnose and describe living and fossil species and revise existing descriptions; to name selected species and genera with descriptions and diagnoses in accordance with current taxonomic practices; and to develop keys and synonymies that are in accordance with demonstrated relationships between the species of Australian Chelids.

The structure of the thesis is by publication. Each chapter represents a discrete piece of research, published in the scientific literature following peer review, and subsequently

included in the thesis for examination. The introduction to the thesis is short, as each chapter has its own introduction, and the thesis ends with a succinct synopsis.

Chapter 2 addresses the uncertainty over a major structural character, the presence or absence of neural bones, thought to be almost universal for Australasian chelid turtles. The research presented in Chapter 2 shows that neural bones are present as sub surface elements of the carapace in all species of Australasian chelid, and that it is in only a few that these elements have a surface expression in what is traditionally scored as presence of neural bones.

Chapter 3 presents evidence for the reassignment of the fossil *Emydura lavarackorum* White & Archer, 1994 to the extant *Elseya lavarackorum* based on an examination of post cranial characters in the fossil and an extant, but at the time, undescribed form (*Elseya* sp. aff. *dentata* Nicholson) of Georges and Adams (1996). Perhaps more importantly, the paper reports a series of newly identified characters for distinguishing between the post-cranial skeletons of short-necked chelid turtles of Australasia. These will be invaluable in assigning fossil material to genus and species in the future.

Chapter 4 expands the set of diagnostic characters presented in Chapter 3, and uses these to describe a new fossil species of *Elseya* from the early Pliocene Bluff Downs Local Fauna, and to determine its affinities among extant forms.

Chapter 5 carries the morphological analysis of Chapters 3 and 4 further to revise the fossil chelid turtles described by C. W. de Vis in 1897.

Chapter 6 describes a new species of freshwater turtle from the Burnett River of coastal Queensland, *Elseya albagula*, a large, predominantly herbivorous species previously regarded to belong to the widespread species *Elseya dentata*.

Chapter 7 describes a new genus of freshwater turtles, *Myuchelys*, to resolve a long acknowledged paraphyly and formally describe and name the *Elseya latisternum* group (Georges and Adams, 1992; 1996). This work led to some controversy in recognizing the new genus in the context of a document circulated by Richard Wells in which he proposed the name *Wollumbinia* for the genus. I acted on the advice of Zootaxa referees, who argued that if I did not regard the document of Wells to be a publication for the purposes of nomenclature, I should not cite it. This was a mistake. Reference to the Wells documents is made in a later publication (Georges and Thomson, 2010), where the issue is dealt with more appropriately.

The chapters are each presented as they appear in print, with minor changes presented in square brackets. Figures and tables have been moved to lie immediately following their first reference in the text. For clarity and ease of reference, the Figure legends and Table captions have been slightly amended in the List of Figures and List of Tables respectively. Nomenclature is that used at the time of publication. Nomenclatural changes to current useage are presented in Appendix A to the thesis.

Chapter 2: Neural Bones in Australian Chelid Turtles

Published as: Thomson, S. and Georges, A. 1996. Neural bones in chelid turtles. *Chelonian Conservation and Biology* 2:82-86.

Abstract

Neurals have been demonstrated to be complex characters in Chelid turtles with one species in Australia demonstrated to have them. In this paper we report findings of a second species with a contiguous series of neural and with the aid of transverse sections demonstrate that they are in fact retained in all chelids. The state of absence seen in most chelids is in fact the neurals forming under the pleural bones which meet in the mid-line. This also explains their occasional presence in species such as *Chelodina longicollis* and further offers explanation for the apparent ease with which contiguous series of exposed neurals may be present or absent across different species.

Introduction

Neural bones are median elements of the turtle carapace overlying the dorsal vertebrae. The ancestral condition is thought to be a series of eight relatively narrow, hexagonal neural bones with short sides anteriorly placed, forming a continuous series from the nuchal bone anteriorly to the first suprapygal posteriorly (Pritchard, 1988). This condition is retained in many extant species of the Bataguridae, Emydidae, and Cheloniidae, but frequently modified, for example, by elimination of elements at the ends of the series, formation of one or more octagonal elements, or alteration to a series of hexagons with short sides posteriorly.

Neural bones are probably structurally important for resisting downward pressure in high-domed species, but may be a disadvantage where lateral forces in flatter forms cause torsion among carapacial elements (Pritchard, 1988). Hence, strong swimmers that move by alternating thrusts of the rear limbs, and marine turtles that alternate strokes on land, tend to have reduced neural series with areas of median contiguity between opposing pleural bones (Pritchard, 1988). Neurals are often seemingly absent in Chelidae, where a fixed pelvic girdle and extensive plastral buttressing provide alternative structural resistances to downward pressure and lateral torsion caused by the sideways action of neck extension and withdrawal.

Absence of neural bones was thought to be characteristic of all Australian chelid turtles (Boulenger, 1889; Waite, 1929; Williams, 1953; Zangerl, 1969) until neurals were reported as a consistent feature of *Chelodina oblonga* from Australia's southwest (Burbidge et al., 1974). Subsequently, neurals were also reported as inconsistent variations in five other

Australian species (*Chelodina novaeguineae*, *C. siebenrocki*, *C. longicollis*, *Elseya latisternum*, and *Elseya* sp.; Rhodin and Mittermeier, 1977). In most cases, however, these neurals were few, small, and rudimentary, not forming a contiguous series.

In this note, we report a second Australian chelid characterized by the consistent presence of well-developed neurals. This feature incidentally provides a morphological basis for separating what was previously a cryptic species pair (Georges and Adams, 1992). We also argue, on examination of sections through the vertebral region, that all chelids possess neural bone elements, but that in those species traditionally regarded as lacking neurals, these elements are so reduced as to be submerged beneath the dorsal medially contiguous pleurals.

Materials and Methods

Specimens were obtained from various collections, skeletonized, and the scutes removed to reveal the arrangement of bony elements. Longitudinal and transverse sections of shell vertebrae and associated neurals and pleurals were prepared with a diamond saw for the chelid turtles *Chelodina longicollis*, *C. oblonga*, *Emydura* sp. aff. *krefftii* (Fraser Island), *Emydura* sp. aff. *subglobosa* (Sleisbeck), and *Elseya dentata*, as well as for the trionychid *Aspideretes hurum*. Where exposed neurals were present, sections were arranged to transect one or more of them. Sections were examined under a microscope to ascertain the presence of sutures between the various elements.

Specimens Examined

All unregistered specimens that remained intact following examination were lodged with the Queensland Museum. The sectioned specimens remain in the collection of the University of Canberra. Names given to undescribed species follow those of Georges and Adams (1992). Abbreviations: AM, Australian Museum; QM, Queensland Museum; NTM, Museums and Art Galleries of the Northern Territory; UM, University of Michigan field series; UC, University of Canberra; PCHP, Peter C.H. Pritchard personal collection. *Chelodina longicollis*: QM 59266-68, 59274, 59281-82, UC 0164,0166, 0174; *Chelodina oblonga*: QM 59272-74, UC0161-63; *Chelodina expansa*: QM59284; *Chelodina rugosa*: QM 59264; *Elseya dentata* (Daly River, N.T.): NTM 13319,13521, 16330,QM59277-80,UCOI79; *Elseya* sp. aff. *dentata* (South Alligator River, N.T.): AM 128002, 128004, QM 59285-88; *Elseya latisternum*: AM 123037, 123039, 125474-75, QM 48054-55; *Elseya* sp. aff. *latisternum* (Manning River, N.S.W.): AM 123040,123042, QM 59289-90; *Elseya* sp. aff. *latisternum* (Bellinger River, N.S.W.): AM 138387-88,UM02016-17; *Elseya novaeguineae* (Sepik River,

New Guinea): AM 42662, 125038; *Emydura* sp. aff. *krefftii* (Fraser Island, Qld.): QM 59275-76; *Emydura* sp. aff. *subglobosa* (Sleisbeck, Katherine River, N.T.): NTM 13428, 13433, UC 0171-72, 0177; *Aspideretes hurum* (no data): UC 0167; *Chelus fimbriatus* (Venezuela): PCHP 3985; *Pelomedusa subrufa* (no data): UC 0221; *Phrynops gibbus* (no data): UC 0222.

Results

Well-developed neural bones forming a contiguous series were observed in specimens of *Aspideretes hurum* (n = 1, pleural pair VIII was in medial contact), *Pelomedusa subrufa* (n = 1, pleural pair VIII was in medial contact), *Chelus fimbriatus* (n = 1, pleural pair VIII was in medial contact), *Phrynops gibbus* (n = 1, pleural pair I and V to VIII were in medial contact), *Chelodina oblonga* (n = 6, pleural pairs I and VIII were in medial contact in all specimens with considerable variation for other pleural pairs), and *Elseya* sp. aff. *latisternum* (Manning River) (n=4, pleural pairs I and VI to VIII were in contact in all specimens and pleural pair V in one specimen and II in two specimens) (Fig. 1). Neural bones were most developed in *Chelus*, being expanded both horizontally and vertically, yielding much enlarged canals for the longissimus dorsi muscles. Rudimentary exposed neurals, small and isolated, were evident as individual variants in *Chelodina longicollis* (1 of 9, UC 0166), *Elseya novaeguineae* (1 of 2, AM 42662), and *Elseya* sp. aff. *dentata* (South Alligator River, N.T.) (1 of 6, QM 59285). Table 1 shows the neural formulae for all these specimens, following the conventions of Pritchard (1988).

No exposed neurals were evident in any of the specimens of *Elseya latisternum* (n=6), *Emydura* sp. aff. *krefftii* (n=2), *Em.* sp. aff. *subglobosa* (Sleisbeck) (n=5), *Elseya* sp. aff. *latisternum* (Bellinger) (n=4) (Fig. 1), *Elseya dentata* (n=8), *Chelodina expansa* (n=1), or *Chelodina rugosa* (n=1).

The presence of well-developed exposed neurals in all four specimens of the undescribed species from the Manning drainage of New South Wales and their absence in all four individuals of its sister taxon (Georges and Adams, 1992) from the Bellinger River was a substantial and significant difference between these sibling taxa (Fisher Exact Test, $P < 0.05$).

A transverse section through the vertebral region of *Aspideretes hurum* revealed a suture between the neural bone and the underlying vertebral neural arch (Fig. 2A). Corresponding sections of a specimen of *Chelodina longicollis* with three exposed neurals revealed sutures similar to those observed in *A. hurum* (Fig. 2B), as did sections of *C.*

longicollis, *Elseya dentata*, and *Em. sp. aff. subglobosa* (Sleisbeck) (Fig. 2C) in the absence of exposed neural bones.

Discussion

This study establishes the undescribed *Elseya* from the Manning drainage of New South Wales as the second Australian chelid with well-developed neural bones. The presence of neurals in this species and their absence in its sister taxon from the Bellinger River is a major discrete morphological difference in what was formerly a cryptic species pair (Georges and Adams, 1992). This species pair shows fixed differences at 20% of electrophoretic loci, despite little if any external morphological difference. This provides an important example of where surveys based on molecular techniques can serve to focus attention on morphological features that might otherwise have gone undetected.

The Manning River *Elseya* has a rather short series of 3 to 5 neurals, a condition similar to that found in *Phrynops gibbus* (Chelidae). There is no obvious lateral expansion of the rib heads to accommodate enlarged *longissimus dorsi* muscles and in fact the ribs fit quite closely to the sides of the neural arches. This combination is also seen in *Pelomedusa subrufa* (Pelomedusidae) and is therefore considered to be the primitive condition.

If the function of well-developed neurals is to add stability to shells particularly subject to lateral torsion (Pritchard, 1988) and this function is supplanted in chelids by the presence of a fixed pelvic girdle and extensive buttressing, then we would expect to see a correlation between the presence of neurals in chelid turtles and the lack of development of plastral buttresses. Indeed, anterior plastral buttressing is poorly developed in *Chelodina oblonga*, compared to other species of similar body form and habits in the *Chelodina expansa* group, and *Chelodina oblonga* has well developed neurals. Similarly, among the short-necked chelid turtles of Australia (excluding *Pseudemydura*), the Manning River form of *Elseya* which has well developed neurals, has the least developed anterior bridge buttresses.

On the basis of the bone sections, we suggest that there are three neural character states:

1. Neural bones small, rudimentary, not visible in dorsal view, being obscured entirely by the pleurals which meet medially for the full length of their common midline suture.

Table 1. Neural formulae of specimens examined possessing exposed neurals. Also shown is the number of pleural pairs which make midline contact. Pleural pairs numbered I to VIII, anterior to posterior.

Species	Specimen	N1	N2	N3	N4	N5	N6	N7	N8	Pleural Pairs in Contact
<i>Aspideretes hurum</i>	UC0167	6P	6P	6P	6P	6A	6A	6A	5A	VIII
<i>Pelomedusa subrufa</i>	UC0221	6A	6A	6A	6A	6A	6A			VIII
<i>Chelodina longicollis</i>	UCOJ66		4	3P	5					ALL
<i>Chelodina oblonga</i>	QM 59283	5P	7A	5A	5A	6A	6A	5A	5	I, VII, VIII
	QM 59272	6P	5P	4A	5A	5A	6A	7A		I, VIII
	QM 59273	6P	5P	4P	4P	5A	5A	5A	3	I, VI, VII, VIII
	UCO163		6A	7A	5A	5A	6A	5A	5	I, VII, VIII
	UCO162		3A	8A	8A		5			I, II, V, VI, VII, VIII
	UCOI61		5A	6P	5A		5A			I, V, VI, VII, VIII
<i>Chelus fimbriatus</i>	PCHP 3985	6P	6A	6A	6A	6A	6A	6A		VIII
<i>Elseya novaeguineae</i>	AM 42662							3		ALL
<i>Elseya</i> sp. (Manning)	AM 123040			6A	6A	6A	6P			I, VI, VII, VIII
	AM 123042			5A	6A	6A	5A			I, II, V, VI, VII, VIII
	QM 59289		5P	6A	6A	6A	5A			I, VI, VII, VIII
	QM 59290		6A	6A	6A	6A	5A			I, II, VI, VII, VIII
<i>Elseya</i> sp. (S. Alligator)	QM 59286							5		ALL
<i>Phrynops gibbus</i>	UC0222	5	6A	6A	6A	6A				I, V, VI, VII, VIII

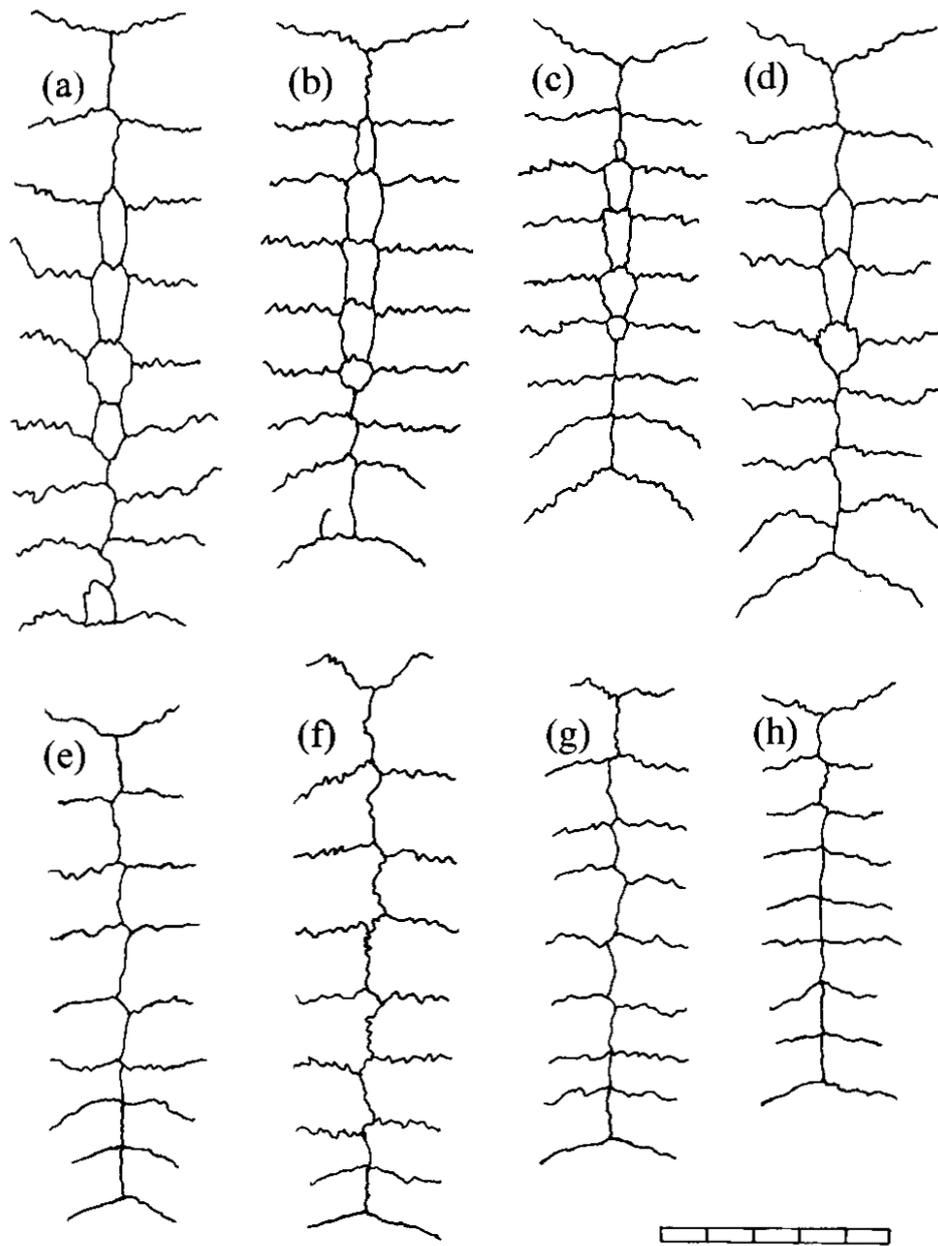


Figure 1. Comparison of the neural region of the dorsal carapace of the sibling species pair *Elseya* sp. aff. *latisternum* (Manning) (upper row, a to d) and *Elseya* sp. aff. *latisternum* (Bellinger) (lower row, e to h). Scale 5 cm. (a) AM 123042, (b) QM 59290, (c) QM 59289, (d) AM 123040, (e) AM 138387, (f) AM 138388, (g) UM 02016, (h) UM 02017.

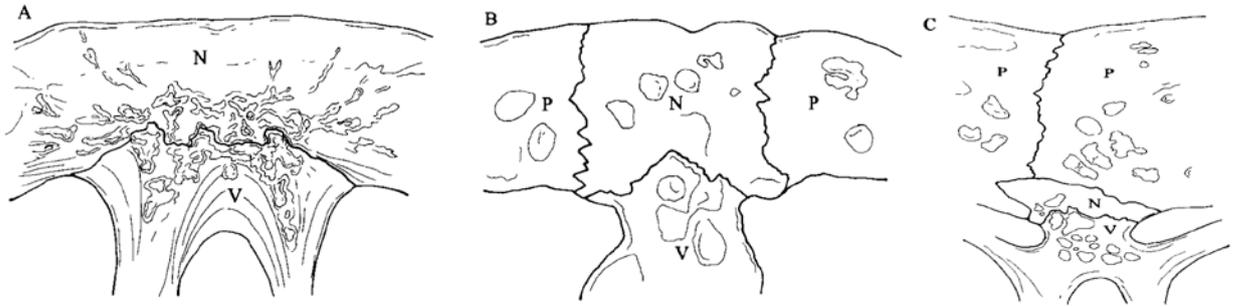


Figure 2. A. Transverse section through the first neural of *Aspideretes hurum* (UC 0167) showing the suture between the wide neural bone (N) and the vertebral neural arch (V). B. Transverse section through carapace of *Chelodina longicollis* (UC 0166) at pleural IV showing a narrow midline neural bone, lateral pleurals (P) and underlying vertebral neural arch. C. Transverse section through *Emydura* sp. aff. *subglobosa* (UC 0177) at pleural IV showing location of a rudimentary neural bone underneath medially contiguous pleurals.

2. Neural bones small, rudimentary, but exposed as small bony elements along the carapace midline. They do not form a contiguous series and pleural to pleural sutures make the predominant contribution to the midline suture.
3. Neural bones well developed and dorsally exposed, forming a contiguous midline series of two or more discrete elements. Pritchard (1988) has further subdivided this character state, based on a study of a greater range of specimens than examined here.

The demonstration of subsurface neural elements suturally separated from the neural arches of the dorsal vertebrae, with the possibility that neurals of some form may be present in all chelids, requires us to rethink our character definitions. The character state "neurals absent" should be instead "exposed neurals absent" and "neurals present" should become "neurals exposed". Also it will be necessary to appreciate that secondary development of exposed neurals may not imply reacquisition of a structure once lost but rather expansion of a persistent but rudimentary element.

Whether the subsurface neural elements are vestigial (that is, lacking function) is not clear. The possibility exists that by spanning the midline carapace suture from below, they reinforce it and relieve lateral pressure that would otherwise come to bear on the neural arches should the shell be subjected to downward force. Such a function would explain their retention.

Matching the distribution of well-developed neurals among chelid turtles with current phylogenetic hypotheses is problematic (Gaffney, 1977). Neurals are well developed in the South American *Chelus fimbriatus*, *Hydromedusa* spp., and the *Phrynops geoffroanus* complex (Rhodin and Mittermeier, 1983; Pritchard, 1988), and in the Australian *Chelodina oblonga* (Burbidge et al., 1974), and *Elseya* sp. aff. *latisternum* (Manning) (present study). The character also shows great individual variability in *Phrynops nasutus* and *P. gibbus* (Pritchard, 1988). Clearly, either loss of exposed neurals has occurred independently many times, or well developed neurals have been secondarily derived independently many times, or a combination of the two is true.

It is not clear whether the well-developed neurals of *Chelodina oblonga* or *Elseya* sp. aff. *latisternum* (Manning) are ancestral or secondarily derived. Consideration of the currently hypothesized phylogeny for Australian chelids (Georges and Adams, 1992) indicates that if exposed neurals are ancestral for both species, then loss of exposed neurals must have

occurred independently at least five times in their evolutionary history, and twice in *Chelodina* alone (Fig. 3, hatched squares).

We suggest instead that the presence of exposed neurals is a retained ancestral state in only *Elseya* sp. aff. *latisternum* (Manning), possessed in common with *Phrynops gibbus* and *Pelomedusa subrufa*, whereas in *Chelodina oblonga* it is secondarily derived. In this scenario, the loss of exposed neurals would have occurred independently only four times, and only once in *Chelodina* (Fig. 3, open squares). Compelling evidence is building to suggest that the closest living relatives of *Chelodina oblonga* are among the *Chelodina longicollis* group of species (including *C. novaeguineae*, *C. steindachneri*, *C. mccordi*, *C. reimanni*, and *C. pritchardi*) rather than the *C. expansa* group to which it bears the closest superficial similarity (including *C. parkeri*, *C. rugosa*, and *C. siebenrocki*). Electrophoretic comparisons yielded five synapomorphies uniting *C. oblonga* with the *C. longicollis* group (Georges and Adams, 1992), a result confirmed by recent comparisons of 12S mitochondrial gene sequences (J. Seddon, pers. comm.). A more distant relationship may explain the presence of well-developed neurals in *C. oblonga* and the absence of exposed neurals in the *C. expansa* group of species.

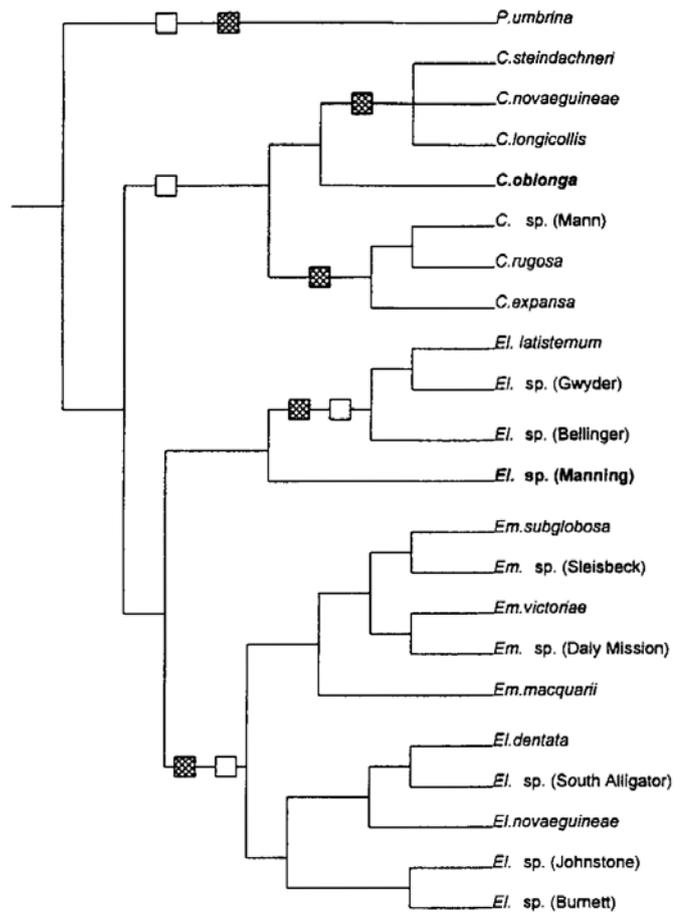


Figure 3. Occurrence of loss of exposed neurals mapped on the currently hypothesized phylogeny of Australian chelids (Georges and Adams, 1992). Open squares assume that in the Manning River *Elseya* neurals are ancestral and in *C. oblonga* they are secondarily derived. Hatched squares assume that both *C. oblonga* and *Elseya* sp. (Manning) retain ancestral neurals. Note: *Elusor macrurus* and *Rheodytes leukops* have been left out of this phylogeny for two reasons, 1) they were inadequately resolved (forming a trichotomy with the *Elseya dentata*; *Emydura* groups) and 2) they will have no effect on the neural character state, both species lacking exposed neurals.

Chapter 3: Re-evaluation of *Emydura lavarackorum*: identification of a living fossil

Published as: Thomson, S.A., White, A. & Georges, A. 1997. Re-evaluation of *Emydura lavarackorum*: Identification of a living fossil. *Memoirs of the Queensland Museum* 42(1): 327-336.

Abstract

Post-cranial osteological characters can be used to diagnose Australian short-necked chelid turtles to genus. Morphological examination of the Pleistocene fossil *Emydura lavarackorum*, from Riversleigh, shows that it is aligned with the genus *Elseya* not *Emydura* and should be referred to as *Elseya lavarackorum* (White & Archer, 1994). Furthermore, the fossil specimen is not distinguishable from an undescribed extant form of *Elseya* from the Nicholson drainage, with which it shares one unique feature so this name should apply also to this extant form, identified to date only from electrophoretic data. It is Australia's first living fossil turtle, an extant population of a Pleistocene taxon.

Keywords: Chelonia, Chelidae, Pleistocene, fossil, turtle.

Introduction

The taxonomy of Australian chelid turtles is poorly known and in dire need of review (Cogger et al., 1983). Recent electrophoretic surveys (Georges & Adams, 1992; 1996) have revealed that in some instances, currently accepted species boundaries are difficult to justify and in others, what are currently regarded as single species are in fact two or more. The detailed morphological analyses required to verify these findings have not been conducted (but see Thomson & Georges, 1996), and until recently it was not possible to distinguish even between extant short-necked genera on the basis of osteological characters (Gaffney, 1977). This paucity of osteological data suitable for distinguishing the extant genera makes the identification of fossil forms, most of which are incomplete specimens, difficult. In many instances, chelid fossils have been assigned to either *Chelodina* or *Emydura*, with little or no evidence presented to eliminate the possibility that the short-necked forms among them may be *Elseya*, *Rheodytes* or *Elusor*.

In 1994 a partial carapace and associated plastron from Riversleigh was described as a new species, *Emydura lavarackorum*, by White & Archer (1994). The fossil specimen was from Terrace Site, a fluvial site on the Gregory River. These authors interpreted the

sediments as being Pleistocene in age because of the presence of remains of *Diprotodon optatum* (White & Archer, 1994). The holotype consists of the anterior half of the carapace with some anterior peripherals and an essentially complete plastron with some pelvic material present. The length of the plastron is 390mm (White & Archer, 1994) which corresponds to a carapace length of approximately 420mm. Two other plastra from the same site were also collected but not described.

White and Archer (1994) assigned the specimen to *Emydura* on the mode of the insertion of the anterior bridge into the ventral surface of the carapace. They found that in the derived state, the anterior bridge is angled steeply backwards towards the rib/gomophosis (called transverse process in White & Archer, 1994), whereas in all other chelids the anterior bridge was found to form a continuous line with the rib/gomophosis.

In this paper, we reassess the generic assignment of the fossil by comparing the fossil material with post-cranial character states we have found useful in separating extant genera of Australian short-necked chelid turtles. We also propose that the fossil taxon is extant, a distinctive, undescribed form closely aligned with *Elseya dentata*.

Materials and Methods

Specimens of each of the short-necked species identified using electrophoresis by Georges and Adams (1996) were obtained from museums, the Conservation Commission of the Northern Territory and the University of Canberra. Where forms have not been included in published keys or descriptions, the specimens were selected from those lodged as vouchers to accompany the electrophoretic data. The specimen collection was supplemented by limited field sampling.

Each specimen was skeletonized by removing excess soft tissue and feeding the remaining carcass to dermestid beetles. The skeletal material was bleached in 5% sodium hypochlorate solution, and the process stopped by immersion in 100% ethanol. Plastra were separated from carapaces by disarticulating the plastral-carapacial suture between the hyo and hypoplastra of the plastron and the lateral peripherals of the carapace. This was done by the carefully heating the carapace until the sutures become mobile and the plastron was then gently prized off. This also required disarticulation of the pelvis from the carapace. Characters potentially diagnostic at the generic level were examined to establish their consistency across a range of specimens within the polytypic genera *Elseya* and *Emydura*, and across a range of specimens within each species.

The fossil specimens of *Emydura lavarackorum* were examined to determine the presence of character states which are generically diagnostic in extant taxa. The fossil specimen was then assigned to genus.

Throughout this paper, we refer to a generic group as a group of species that are sufficiently distinct collectively to warrant recognition at the level of genus, though this has not yet been formally established. These groups were first identified by Legler (1981), have a foundation in electrophoretic studies (Georges & Adams, 1996), and have been referred to since several times in the literature. In contrast, a species complex is a group of species, all but one of which are undescribed, which together presumably represent a distinct clade but which are not considered distinctive enough to warrant recognition at the level of genus.

We refer to the *Elseya dentata* species complex as comprising the distinctive forms of *Elseya* from coastal Queensland currently assigned to *Elseya dentata*, and the Northern Territory forms including *Elseya dentata* (sensu stricto) and *Elseya* sp. aff. *E. dentata* from the Alligator Rivers region (Georges & Adams, 1996). The *Elseya dentata* generic group (sensu Legler, 1981) comprises the *Elseya dentata* species complex plus *Elseya novaeguineae* and *Elseya branderhorsti* from New Guinea. The *Elseya latisternum* generic group comprises *Elseya latisternum* (sensu stricto), a related form from the head waters of the Darling River drainage and a sibling species pair from coastal New South Wales (Georges & Adams, 1996; Thomson & Georges, 1996). The later three are currently undescribed. It is not the purpose of this paper to describe new genera, so for consistency, we use the nomenclature of Georges & Adams (1992) and Legler (1981) and recognize six groups of Australian short-necked chelid at generic level: *Elusor*, *Emydura*, *Rheodytes*, *Pseudemydura*, the *Elseya latisternum* generic group and the *Elseya dentata* generic group.

Throughout this paper, names of the bony elements of the shell and the overlying scutes follow those of Zangerl (1969). A complete list of the specimens examined in this study will be found in Appendix A.

Results

Five characters were identified as diagnostic at generic level. Where polarity is indicated, it was determined by comparison with South American chelids and African pelomedusids in a cladistic analysis (Thomson & Georges, unpublished data). Only those characters relevant to the identification of the fossil specimen are presented.

ANTERIOR BRIDGE STRUTS.

Character A. Contact with Pleural 1.

- A0. In the primitive state, the posterior edge of the bridge-carapace suture runs parallel and adjacent to the rib/gomphosis of pleural1 (Fig. 1 A-F).
- AI. In the derived state, the posterior edge of this suture contacts the rib/gomphosis at its anterior end, but is set at a forward divergent angle of between 15 and 50°. This angle is most pronounced in *Emydura*, least in *Rheodytes* (Figs 2A-F, 3A-D).

Character B. Bridge suture shape.

- B1. The anterior and posterior edges of the bridge-carapace suture diverge from their point of congruence closest to the vertebral column. The widest extent of the suture is distal to the vertebral column and there is no medial constriction (Fig. 1A-F)
- B2. The anterior and posterior edges of the bridge-carapace suture are parallel or closely so with a prominent suture surface between them. There is no medial constriction (Figs 2A-B, E-F, 3A-B).
- B3. The bridge-carapace suture is expanded for its full length, but more so at extremes, there being an obvious medial constriction (Fig. 2B).
- B4. The bridge-carapace suture narrows from its widest point proximal to the vertebral column, and constricts completely to form a ridge confluent with the edge formed by the ventral suture of the peripheral bones (Fig. 3C-D).

RIB/GOMPHOSIS OF PLEURAL I.

Character C. Rotation of the Rib/Gomphosis.

- C0. The ventral surface of the distal extent of the rib/gomphosis is rotated obliquely, to face ventrally but with posterior inflection (Figs I A-F, 2A-B).
- C1. The rib/gomphosis shows no such torsion distally (Figs 2C-F, 3A-D).

DORSAL CHARACTERS.

Character D. Relative width of Vertebral I.

D1. 1st 3 vertebral scutes equal or sub equal in width (Figs 4A-D, 5B).

D2. 1st vertebral scute wider than 2nd and 3rd (Figs 4E-F, 5A).

Character E: Cervical Scute.

E0. Cervical scute typically present (Fig. 5B).

E1. Cervical scute typically absent (Figs 4E-F, 5A).

The distribution of the character states for each taxon is provided in Table 1. The holotype *Emydura lavarackorum* had a combination of a widely divergent angle (45°) between the anterior bridge suture and the rib/gomphosis of pleural one; parallel anterior and posterior edges of the bridge-carapace suture throughout their length, widely spaced, with no medial constriction; no distal rotation of the gomphosis of pleural one; a first vertebral scute that was markedly wider than vertebrals 2 and 3; and no cervical scute. A significant feature of *Emydura lavarackorum*, though difficult to quantify, was an indentation of the carapace margin in the area of the cervical cleft and first marginal scutes. This feature is held in common with turtles in the *Elseya latisternum* group and *Pseudemydura*, is variable among the Queensland forms of *Elseya dentata*, and never present in the Northern Territory and New Guinea forms of *Elseya dentata* nor in *Elusor*, *Rheodytes* and *Emydura*. Although not considered a useful character at generic level, we will use it in combination with other similarities to establish a close relationship between the fossil *Emydura lavarackorum* and an extant form of *Elseya* from the Nicholson River.

Discussion

The bridge carapace suture runs parallel and adjacent to the rib/gomphosis in species of the *Elseya latisternum* group, *Pseudemydura* and *Elusor* and so can be clearly distinguished from the fossil *Emydura lavarackorum* (Table 1). Rotation of the rib/gomphosis of Pleural 1 eliminates *Rheodytes* as a possible identification for the fossil, leaving only the *Elseya dentata* generic group and *Emydura* as possibilities.

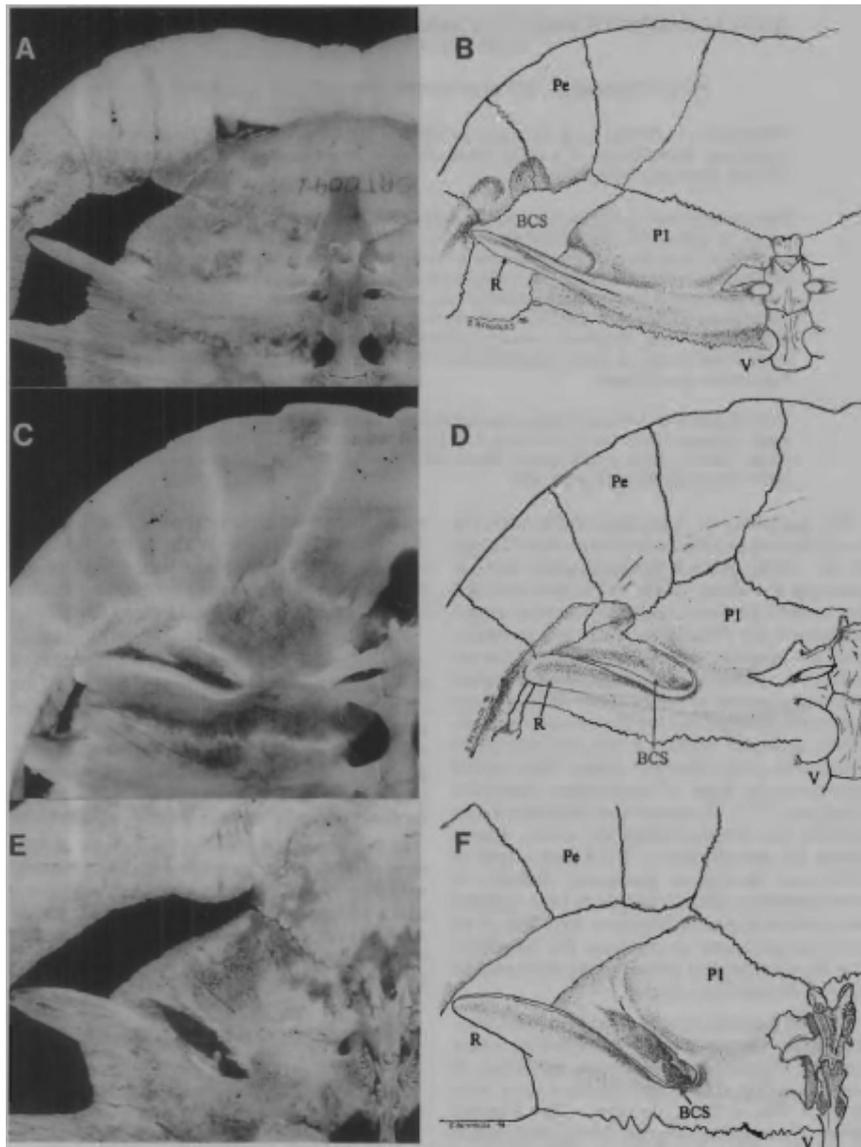


Figure 1. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomphosis (R) on pleural 1 (P1) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B. *Pseudemydura* (UC0178). C-D *Eelseya* sp. aff. *E. latisternum* (Manning) (QM59289); E-F, *Elusor macrurus* (UC0184).

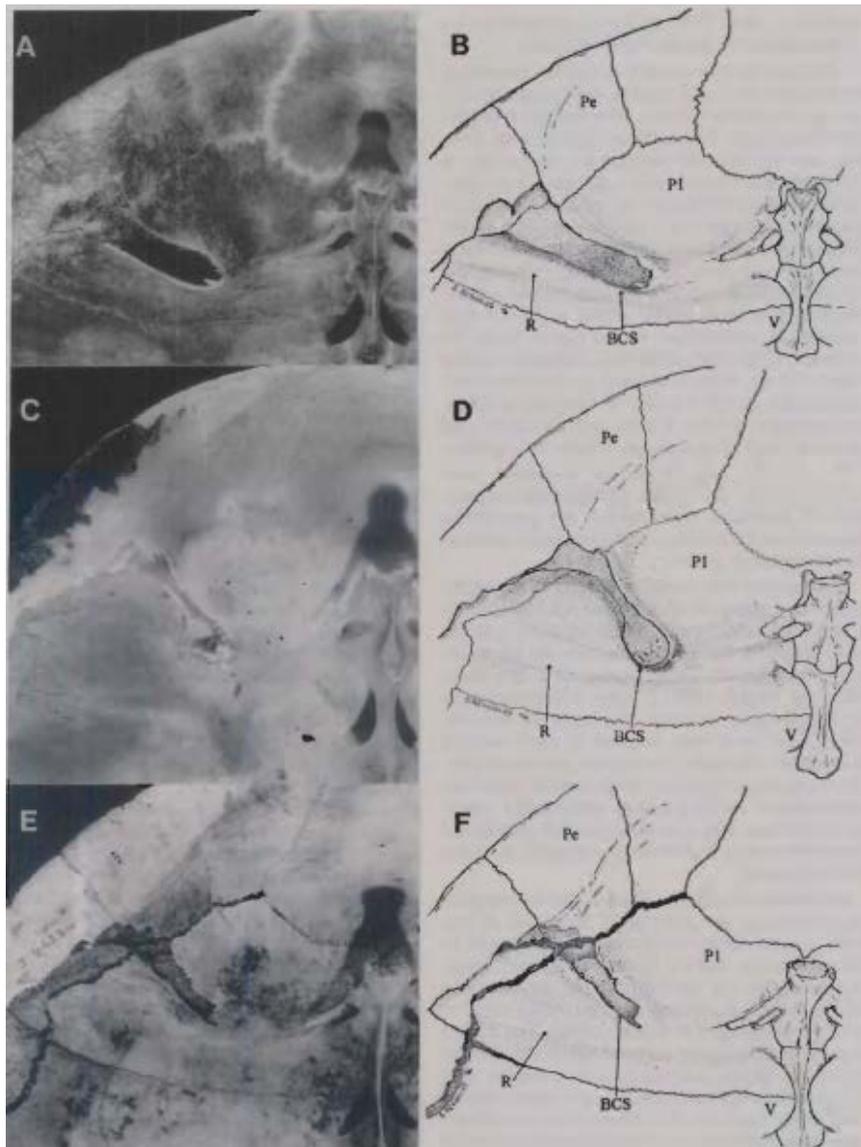


Figure 2. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomphosis (R) on pleural 1 (P1) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B, *Rheodytes leukops* (UC0173). C-D, *Elseya dentata* (QM59277). E-F, *Elseya lavarackorum* (extant) (QM46284).

Table 1. Character Matrix. Distribution of the key character states among taxa. Abbreviations (s = No. of species examined in group, n = No. of specimens), polymorphic characters shown: Pseud, *Pseudemydura*; Elat, *Elseya latisternum* group; Elus, *Elusor*; Rheo, *Rheodytes*; Else, *Elseya dentata* group; Elno, *Elseya novaeguineae*; EQld, Queensland *Elseya* group; Elav, *Elseya lavarackorum* (holotype); Emyd, *Emydura*.

Taxa	Pseud (s=1) (n=2)	Elat (s=4) (n=20)	Elus (s=1) (n=18)	Rheo (s=1) (n=1)	Else (s=2) (n=25)	Elno (s=1) (n=2)	EQld (s=3) (n=10)	Elav (s=1) (n=1)	Emyd (s=4) (n=28)
Character A	0	0	0	1	1	1	1	1	1
Character B	1	1	1	2	3	3	2	2	4
Character C	0	0	0	0	1	1	1	1	1
Character D	1	1	1	1	2	2	2	2	1
Character E	0	01	0	0	1	0	1	1	0

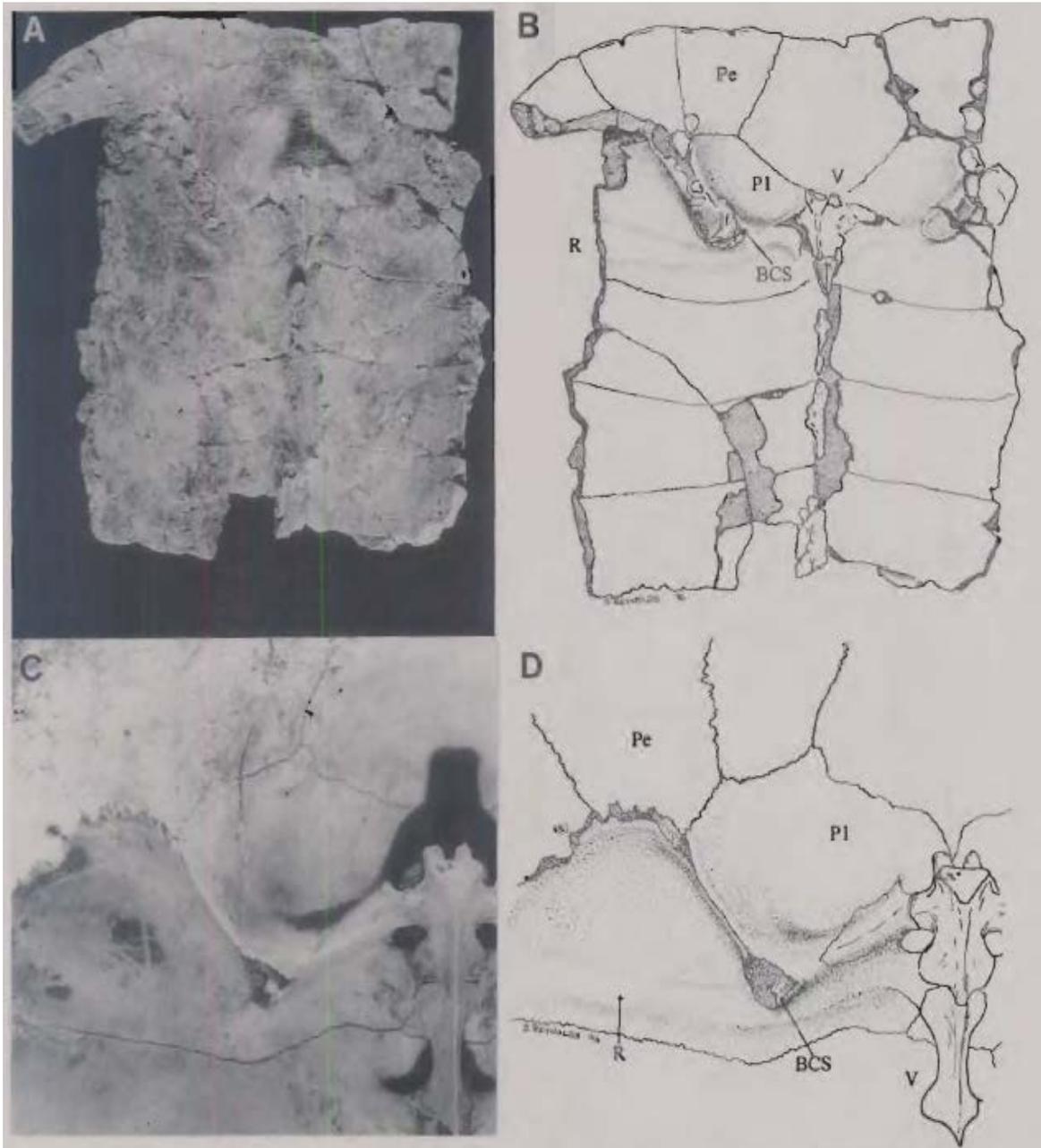


Figure 3. Ventral view of the anterior carapace of short-necked turtles showing the bridge-carapace suture (BCS) the rib/gomphosis (R) on pleural 1 (P1) and their relationship to the vertebral column (V) and the peripherals (Pe). A-B, *Elseya lavarackorum* (fossil) (QM24121). C-D, *Emydura subglobosa* (UCOI72).

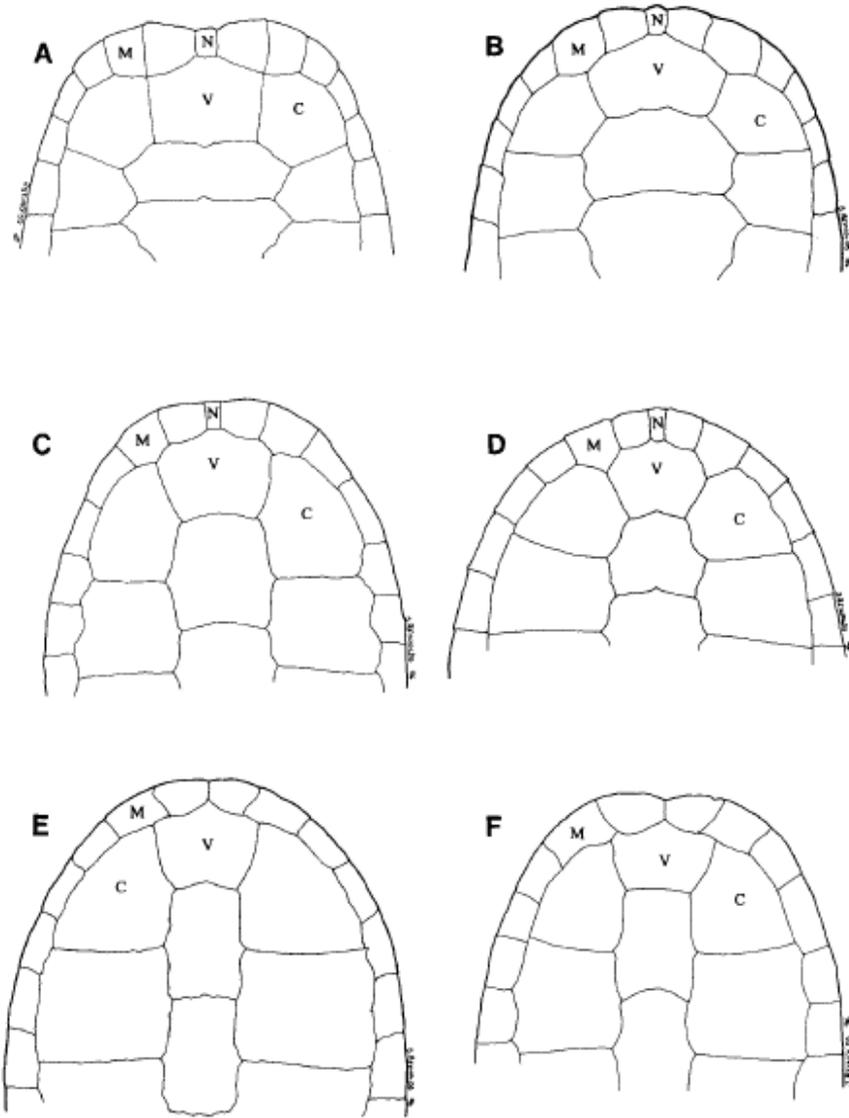


Figure 4. Dorsal view of the anterior carapace of short-necked turtles showing the relative size between the vertebral scutes (V) and the presence or absence of the cervical scute (N) their relationship to the costal scutes (C) and marginals (M). Note the indentation at the anterior of some taxa. A. *Pseudemydura* (UC0178). B. *Ealseya* sp. aff. *E. latisternum* (Manning) (QM59289). C. *Elusor macrurus* (UC0344). D. *Rheodytes leukops* (UC0173). E. *Ealseya dentata* (QM59277). F. *Ealseya lavarackorum* (extant) (QM46284).

Two sub-groups within the *Elseya dentata* generic group can be distinguished. The first comprises *Elseya dentata* (sensu stricto), *Elseya novaeguineae*, *Elseya branderhorsti*, and *Elseya* sp. (Vogelkopf Region, PNG; Anders Rhodin, pers. comm.) and *Elseya* sp. (South Alligator River, NT; Georges & Adams, 1996). The second sub-group is restricted to Queensland (Queensland *Elseya dentata* sub-group) and comprises *Elseya* sp. (Nicholson), *Elseya* sp. (Johnstone), and *Elseya* sp. (Burnett) (Georges & Adams, 1996). Generic recognition of these sub-groups is not suggested.

Emydura lavarackorum possesses all characters that are consistent across species of the *Elseya dentata* generic group (Table 1) and, more significantly, all characters uniquely possessed by the Queensland *Elseya dentata* sub-group (Table 1). Of those characters which separate *Emydura* from the *Elseya dentata* generic group, the fossil consistently possessed character states which distinguished it from *Emydura*. Therefore, we assign *Emydura lavarackorum* to the genus *Elseya* as *Elseya lavarackorum* (White & Archer, 1994).

Since the description of *Elseya lavarackorum*, specimens of the extant *Elseya* sp. (Nicholson drainage, Georges & Adams, 1996) have become available. The two forms are indistinguishable in every diagnostic character, including the indentation of the anterior margin of the carapace. A unique feature of the Nicholson population, when only extant forms are considered, is the sigmoidal shape of the sulcus between the humerals and pectorals on the plastron (Fig. 5C), this sulcus is straight in all other species of the *Elseya dentata* generic group (Fig. 5E). This feature is present in the holotype of *Elseya lavarackorum* (White & Archer, 1994) and in one (QM30818) of the additional fossil specimens now available (Fig. 5D). The anterior plastron is absent from the third fossil specimen (QM30817).

In contrast, the fossil has strongly embossed, rounded peripherals in the region adjacent to the bridge, a feature not present in the 15 specimens from the Nicholson population. This is a similar condition to that found in aged, adult individuals in a number of species, i.e., individuals which are large for their species, such as *Elusor macrurus* (specimens over 400mm), *Elseya* sp. aff. *E. dentata* from the Burnett River (specimens over 380 mm) and *Emydura subglobosa* from the Gregory and Reynolds Rivers (specimens over 250mm). We consider this trait to be essentially a feature of large aged specimens in a range of chelid turtles. None of the turtles examined from the Nicholson drainage had carapace lengths in excess of 320 mm, well below the maximum size for species in the *Elseya dentata* generic group.

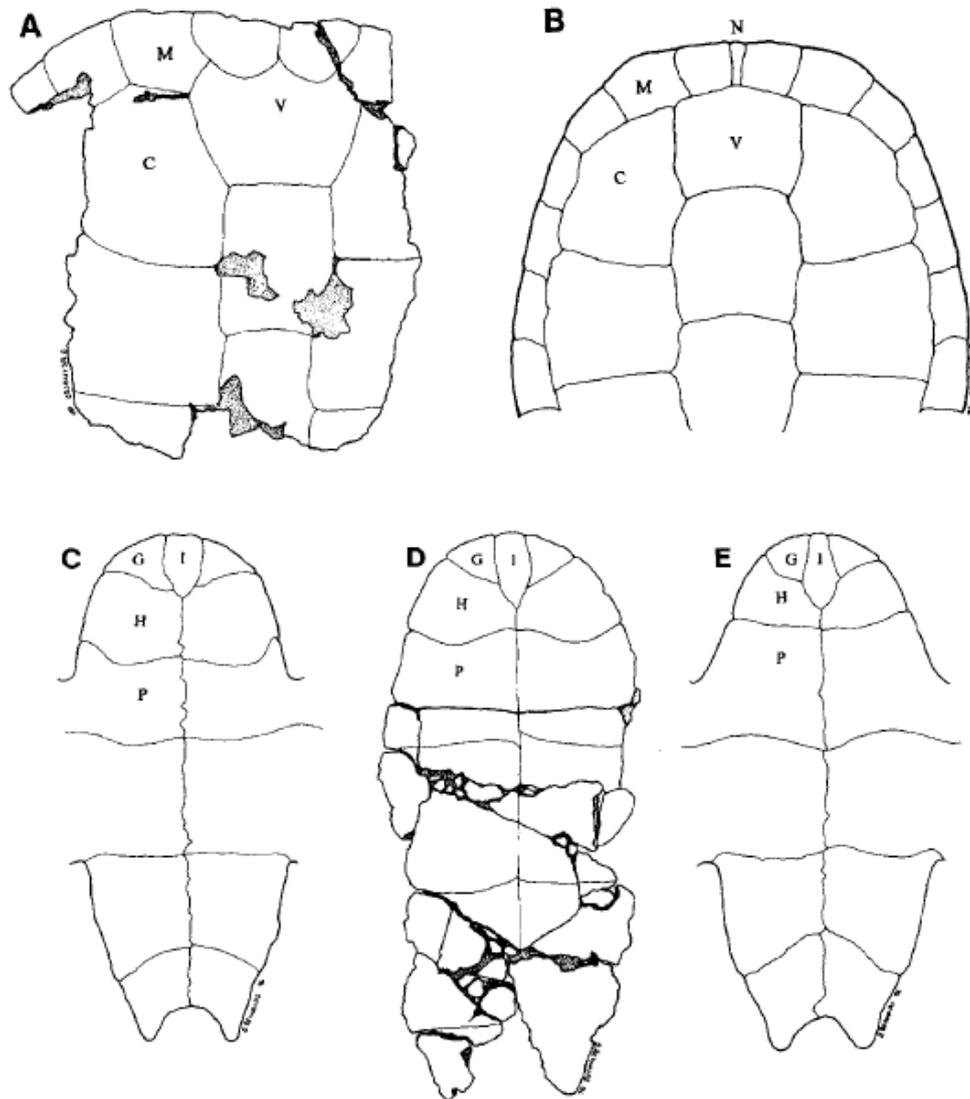


Figure 5. A-B, Dorsal view of the anterior carapace of short-necked turtles showing the relative size between the vertebral scutes (V) and the presence or absence of the cervical scute (N) their relationship to the costal scutes (C) and marginals (M). Note the indentation at the anterior of some taxa. A. *Elseya lavarackorum* (fossil) (QM24121). B. *Emydura subglobosa* (UC0172). C-E, Ventral view of the plastrons showing the arrangement of the sulci between the humeral (H) and pectoral (P) scutes, also shown are the gular scutes (G) and the intergular (I). C. *Elseya lavarackorum* (extant) (QM46284); D. *Elseya lavarackorum* (fossil) (QM24121). E. *Elseya dentata* (QM59277).

In species level taxonomy, the onus is on differential diagnosis. The shell of the fossil holotype is adequately preserved for diagnostic purposes. We therefore propose that, in the absence of any diagnosable difference and the relatively young age of the fossil material, *Elseya lavarackorum* and the Nicholson *Elseya* sp. aff. *E. dentata* be regarded as a single species. It is Australia's first living fossil freshwater turtle, an extant population of a Pleistocene taxon. We do not propose that allochronic subspecies be recognised.

Appendix A: Specimens Examined.

All names used for undescribed species are from Georges & Adams (1992, 1996).
Abbreviations used: AM, Australian Museum; NTM, Museum and Art Galleries of the Northern Territory; QM, Queensland Museum; WAM, Western Australian Museum; UC, University of Canberra; UM, University of Michigan Field Series; UU, University of Utah.

Elusor macrurus: UCO184-93, 0225-29, 0344, UU19488, 19508.

Elseya dentata: NTM13319, 13521, 16330, QM59265, 59277-80, UC0307-18.

Elseya latisternum: AMI23037, 123039, 125474-75, QM48054-55.

Elseya novaeguineae: AM42662, 125038.

Elseya lavarackorum: QMF24121, F30817-I8 (fossil), QM31939, 31942, 31944, 31946-47, 31949-50, 31952, 46284, 47908, 47911, 48544, 48547, 60255, UC0201 (extant).

Emydura macquarii: QM48016, 48034, 48050-51, 59275-76, UC0175-76, 0303.

Emydura subglobosa: NTM5028, 8206, 13428, 13433, 16332, IJC0171-72, 0177.

Emydura victoriae: NTMI3513-14, 32917, 32976, UC 0165.

Elseya sp. aff. *E. dentata* (Burnett): UC 0305-6, QM2966, 28449, 36036, 36039, 36041-42, 36044-47, 37933, 38533, 59269-71.

Elseya sp. aff. *E. dentata* (Johnstone): QM22694, 23175, 23299, 23300, 23322, 24938, 28449, 48060, 48068.

Elseya sp. aff. *E. dentata* (South Alligator): AM 128002, 128004, QM59285-89, NTM5097, 13512, 13985, IJC0304.

Elseya sp. aff. *E. latisternum* (Gwyder): AM 123028-29, QM 48028, 48038.

Elseya sp. aff. *E. latisternum* (Bellingen): AM138387-88, UM02016-17.

Elseya sp. aff. *E. latisternum* (Manning): AM123040, 123042, QM-59289-90.

Emydura sp. aff. *E. victoriae* (Daly Mission) AM125470-71, 125491, NTM8211. 8213, 17339.

Pseudemydura umbrina: UCOI78, WAM29337.

Rheodytes leukops: UCO 173.

Chapter 4: Fossil turtles from the early Pliocene Bluff Downs Local Fauna, with a description of a new species of *Elseya*

Published as: Thomson, S. A. and Mackness, B. S. 1999. Fossil turtles from the Early Pliocene Bluff Downs Local Fauna, with a description of a new species of *Elseya*. *Transactions of the Royal Society of South Australia* 123(3): 101-105.

Abstract

The freshwater turtle fauna of the early Pliocene Bluff Downs Local Fauna consists of members of the *Emydura*, *Chelodina* and *Elseya* genera. A new species of the chelid genus *Elseya* is described based on a partially articulated carapace and associated plastron. The new species is most similar to the living *Elseya irwini* Cann, 1998 but can be distinguished from it by the close encroachment of the ilium suture to the seventh pleural. It also differs from *E. irwini* in having a very narrow ilium suture, almost approaching the *Emydura* condition in this character. Two additional fossil chelids are described.

Keywords: Pliocene, Bluff Downs Local Fauna, chelids, *Emydura*, *Chelodina*, *Elseya*, turtles.

Introduction

Australian chelid turtle taxonomy is poorly known and much in need of review (Cogger et al. 1983; Thomson et al. 1997). Electrophoretic surveys have revealed that in some instances, currently accepted species boundaries are difficult to justify and what are currently regarded as single species are in fact two or more species (Georges & Adams 1992, 1996). The detailed morphological analysis required to verify these findings has not been completed (Thomson & Georges, 1996; Thomson et al. 1997), and until recently it was not possible to distinguish even between extant short-necked genera on the basis of osteological characters (Gaffney 1977). The poor knowledge of osteological characters suitable for distinguishing the genera of extant forms makes the identification of fossils, many incomplete, difficult (Thomson et al. 1997). In many instances, chelid fossils have been assigned to either *Chelodina* or *Emydura*, with little or no evidence presented to eliminate the possibility that the short-necked forms among them may be *Elseya*, *Rheodytes* or *Elusor*.

Materials and Methods

Specimens of the chelid turtle species identified using electrophoresis by Georges & Adams (1996) were obtained from museums, the Conservation Commission of the Northern Territory

and the University of Canberra. Where possible, the voucher specimens of Georges & Adams (1992, 1996) were utilized to avoid incorrect identification. The specimen collection was supplemented by limited field sampling. All specimens were skeletonized and assessed by methods outlined in Thomson et al. (1997).

The fossil specimens from Bluff Downs were collected as part of an on-going study of the paleoecology of the Bluff Downs Local Fauna by one of the authors (BM). Specimens will be deposited in the Queensland Museum. Each was examined to determine the presence of character states for the characters identified as being diagnostic at the level of genus for extant taxa. The fossil specimens were then assigned to genus. Throughout this paper, names of the bony elements of the shell and the overlying scutes follow those of Zangerl (1969) except that we follow Pritchard & Trebbau (1984) and recognize the term pleural as referring to the bones of the carapace rather than the scutes. Additional terminology referring to the anterior bridge struts of the plastron and the bridge strut suture of the carapace follows Thomson et al. (1997).

Five characters were identified as diagnostic at generic level. Where polarity is indicated, it was determined by comparison with South American chelids and African pelomedusids in a cladistics analysis to be presented elsewhere (Thomson & Georges unpub.). Only those characters relevant to the identification of the fossil specimen are presented.

Anterior bridge struts

Character A. Contact with Pleural 1.

A0: In the primitive state, the posterior edge of the bridge-carapace suture runs parallel and adjacent to the rib/gomphosis of pleural 1.

A1: In the derived state, the posterior of this suture contacts the rib/gomphosis at its anterior end but is set at a forward divergent angle of between 15° and 50°.

This angle is most pronounced in *Emydura*, least in *Rheodytes*.

Character B. Bridge suture shape.

B1: The anterior and posterior edges of the bridge- carapace suture diverge from their point of congruence closest to the vertebral column. The widest extent of the suture is distal to the vertebral column and there is no medial constriction.

B2: The anterior and posterior edges of the bridge- carapace suture are parallel or closely so with a prominent suture surface between them. There is no medial constriction.

B3: The bridge-carapace suture is expanded for its full length but more so at extremes, there being an obvious medial constriction.

B4: The bridge-carapace suture narrows from its widest point proximal to the vertebral column and constricts completely to form a ridge confluent with the edge formed by the ventral suture of the peripheral bones.

Rib/gomphosis of pleural 1

Character C. Rotation of the Rib/ Gomphosis

C0: The ventral surface of the distal extent of the rib/gomphosis is rotated obliquely, to face ventrally but with posterior inflection.

C1: The rib/gomphosis shows no such torsion distally.

Dorsal characters

Character D. Relative width of Vertebral 1

D1: First three vertebral scutes equal or sub-equal in width.

D2: First vertebral scute wider than second and third.

Character E. Cervical Scute

EO: Cervical scute typically present.

E I: Cervical scute typically absent.

Posterior internal carapace characters

Character F. Carapace Pelvis Suture

F0: Ilium sutures to the seventh and eighth pleurals and the pygal.

F1: Ilium sutures to the eighth pleural and pygal only but is directly adjacent to the suture between the seventh and eighth pleurals.

F2: Ilium sutures to the eighth pleural and pygal only but is widely separated from the suture between the seventh and eighth pleural.

Comparative material

All names used for undescribed species are from Georges & Adams (1992, 1996) with modifications from Thomson et al. (1997). Abbreviations used: AM, Australian Museum; NTM, Museum and Art Galleries of the Northern Territory; QM, Queensland Museum; WAM, Western Australian Museum; UC, University of Canberra; UM, University of Michigan Field Series; UU, University of Utah.

Elusor macrurus: UC 0184-93, 0225-29 UU 19488, 19508; *Elseya dentata*: NTM 13319, 13521, 16330, QM 59265, 59277-80, UC 0307-18; *Elseya georgesii*: AM 138387-88, UM 02016-17; *Elseya irwini*: ANWC 0520; *Elseya lavarackorum*: QM F24121, QMJ 31939, 31942, 31944, 31946-47, 31949-50, 31952, 46284, 47908, 47911, 48544, 48547, 60255, UC0201; *Elseya latisternum*: AM 123037, 123039, 125474-75, QM 48054-55; *Elseya novaeguineae*: AM 42662, 125038; *Elseya purvisi*: AM 123040, 123042, QM 59289-90; *Emydura macquarii*: QM 48016, 48034, 48050-51, 59275-76, UC 0175-76, 0303; *Emydura subglobosa*: NTM 5028, 8206, 13428, 13433, 16332, UC 0171-72, 0177; *Emydura tanybaraga*: AM 125470-71, 125491, NTM 8211, 8213, 17339; *Emydura victoriae*: NTM 13513-14; 32917, 32976, UC 0165; *Elseya* sp. aff. *E. dentata* (South Alligator): AM 128002, 128004, QM 59285-89, NTM 5097, 13512, 13985, UC 0304; *Elseya* sp. aff. *E. latisternum* (Gwyder): *Elseya* sp. aff. *E. lavarackorum* (Burnett) UC 0305-6, QM 2966, 28449, 36036, 36039, 36041-42, 36044-47, 37933, 38533, 59269-71; *Elseya* sp. aff. *E. lavarackorum* (Johnstone): QM 22694, 23175, 23299, 23300, 23322, 24938, 28449, 48060, 48068, AM 123028-29, QM 48028, 48038; *Pseudemydura umbrina*: UC 0178 WAM 29337; *Rheodytes leukops*: UC 0173.

Systematics

Order Testudines Linnaeus, 1758

Suborder Pleurodira Cope, 1864

Family Chelidae Ogilby, 1905

Elseya nadibajagu sp. nov. . (Figure 1)

Holotype: QM F30576, a partially articulated carapace and associated plastron collected by H. Godthelp during the 1992 Field Season. Upper Andrews Quarry.

Referred specimens: QM F30577 also collected at, the same site.

Type Locality: Upper Andrews Quarry (19° 43' S, 145° 36' E). Allingham Formation, Bluff Downs, Bluff Downs Station, north-eastern Queensland. The Allingham Formation was named by Archer & Wade (1976) for a sequence of terrigenous clays, silts, sands and calcareous sands that outcrop on Bluff Downs Station along the banks of the Allingham Creek, a tributary of the Burdekin River. Several different quarries have been established to exploit these outcrops all showing a similar and contiguous stratigraphy (BM unpub.). The sediments recovered are fluvial and lacustrine in nature and represent a number of depositional events.

Age: Early Pliocene based on the radiometrically dated age of the overlying basalts (Archer & Wade 1976; Mackness et al. [2000])

Diagnosis: The fossil is identified as an *Elseya* by the presence of steeply angled bridge struts features diagnostic of *Elseya sensu stricto*, (Thomson et al. 1997; Thomson [2000a]) and *Emydura*. The carapace sutures for these struts are wide throughout their length, which is diagnostic of the *Elseya lavarackorum* group within this genus (Thomson et al. 1997). Other diagnostic features include the first vertebral scute being wider than the second and third and the absence of a cervical scute (Thomson et al. 1997; Thomson [2000a]). Within *Elseya*, this species is most similar to *E. irwini* (Cann, 1998) from the Burdekin River but can be distinguished from it by the close encroachment of the ilium suture to the seventh pleural. In *E. irwini* the suture is widely spaced as is typical of *Elseya* but in *E. nadibajagu* they are extremely close, almost approaching the *Emydura* condition in this character.

Description

Carapace consists of a complete nuchal bone with no cervical scute present. The left pleural one is more complete than the right and the anterior bridge strut has a wide suture surface between parallel anterior and posterior edges of the suture throughout its length, which is preserved. The suture is deeply inserted into the carapace and angled sharply away from the rib/gomphosis. The sulci preserved in this region indicate that the first vertebral scute was wider than the second and third.

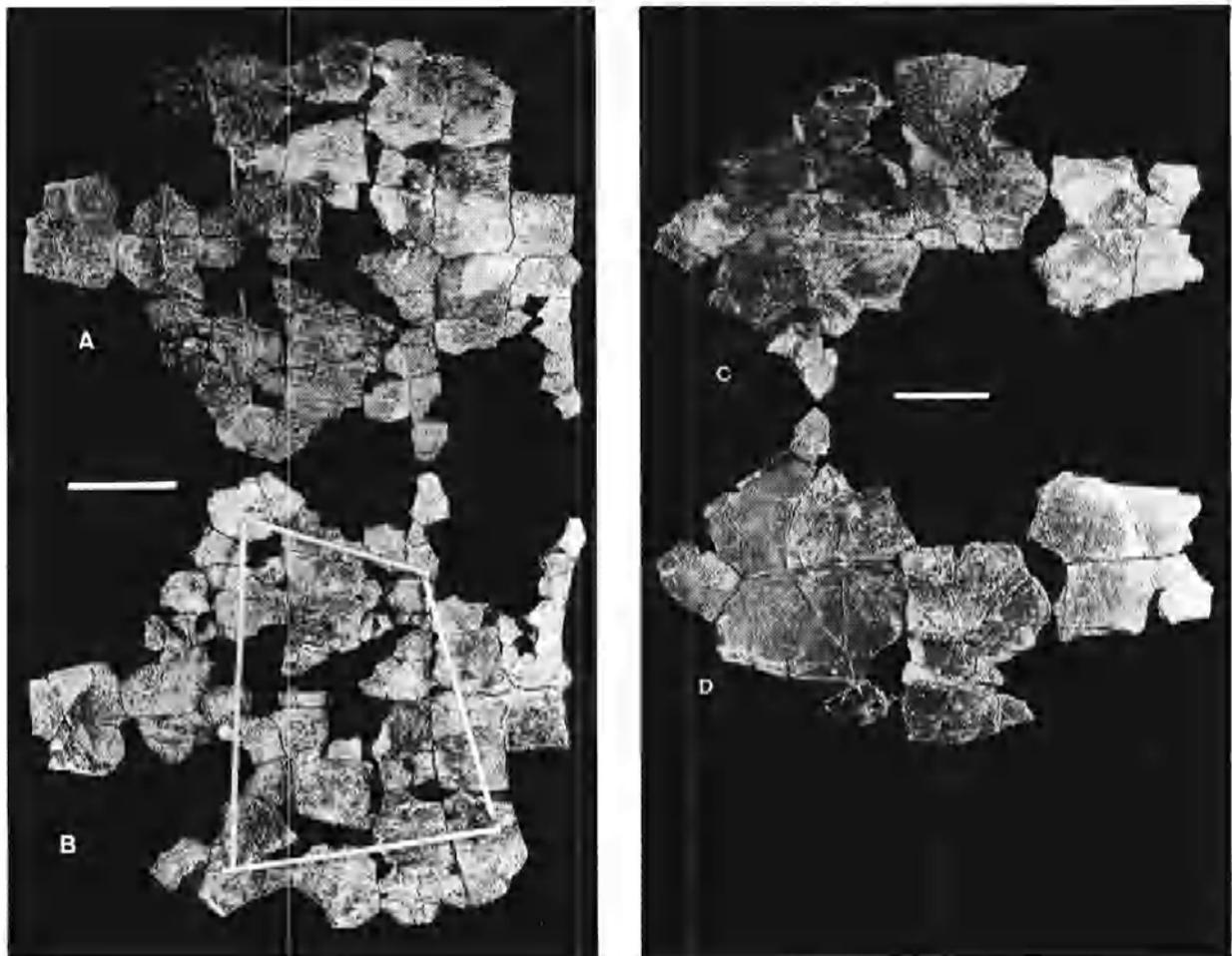


Figure 1. Holotype of *Elseya nadibajagu* sp. nov. (A).External view of carapace. (B). Internal view of carapace. (C). I internal view of plastron. (D) External view of plastron. Scale bars = 5 cm.

Pleurals two to six are partially preserved on either side but without their peripheral contacts. Also preserved as an unarticulated unit is the left eighth peripheral. The anterior suture surface for the ilium is clearly constrained to this unit and does not extend on to, or make suture contact with, the seventh pleural. It does, however, continue on to the pygal in the posterior, the typical condition of the Chelidae. All the units are represented in the plastron except the epiplastra, which are either both missing, or not identifiable among the fragments.

Included here also are both bridge struts. The bridge struts are wide throughout the length at the suture surface where they contact the carapace. The plastral elements, both in sulci and bony elements are similar in form to any extant member of the *Elseya lavarackorum* group.

Etymology

The specific epithet is from the Gugu-Yalanji dialect phrase *nadi bajagu*, meaning 'very long time ago' (Oates et al. 1964) and is used to denote the significant age of the fossil. The name is of neuter gender.

***Chelodina* sp.**

Material examined: QM F30578, an isolated nuchal bone from a long-necked turtle of the *Chelodina longicollis* group.

Remarks

This specimen can be diagnosed by the extreme widening of the posterior half of the nuchal bone as well as the wide, square cervical scute. There is also a large series of muscle attachments for the muscles at the base of the neck which, by necessity, are enlarged in the long-necked turtles (Thomson & Georges 1996). The placement within the *C. longicollis* group is based on the sculptured surface of the shell, a feature more prevalent in species such as *C. longicollis* and *C. novaeguineae* than in members of the *C. expansa* group. This is, however, a highly variable character and probably of poor taxonomic value (Gaffney 1981; Thomson [2000a]).

Emydura macquarii

Material examined: QM F 30579, a series of pleurals all diagnostic of the genus *Emydura* using the bridge strut characters of Thomson et al. (1997).

Remarks

None of the pleurals is distinguishable from those of extant species in the area, *Emydura macquarii* (= *E. krefftii*, Georges & Adams 1996) and we therefore take the most parsimonious view and assign the fossil to the living species which is found in Allingham Creek today.

Discussion

The living species that most closely resembles *Elseya nadibajagu* sp. nov. is *E. irwini* described by Cann (1998) on the basis of its head color. Georges & Adams (1996) have confirmed the validity of *E. irwini* on the basis of electrophoretic studies. Both of these taxonomic indicators (head color and biochemistry) have not been preserved in the fossil material. The use of osteological characters, such as the position of the ilium/carapace suture, has enabled the separation of *E. nadibajagu* from other members of the genus *Elseya*. There is a possibility, however, that this character may be subject to a lot more variation than can be seen in the limited sample of both *E. irwini* and *E. nadibajagu*, although analyses of variation present in other members of the genus makes this unlikely. Reptiles have a lower rate of species turnover than their mammalian counterparts with many extant species having fossil records stretching back millions of years (La Duke 1991).

White & Archer (1994) described the fossil chelid *Emydura lavarackorum* from the Pleistocene deposits of Riversleigh and living examples were described just three years later (Thomson et al. 1997).

The occurrence of three different chelid taxa from Bluff Downs is not unusual with tropical river systems having four or more different genera in the one region (Legler & Georges 1993). There have been five different turtles recorded for the Burdekin (Cann 1998) including three short-necked and two long-necked taxa.

The palaeoenvironment of the Bluff Downs local fauna has been interpreted as being similar to that in present day Kakadu (Boles & Mackness 1994) with avian species such as darters and pygmy-geese indicating permanent water bodies (Mackness 1995). There may have also been riparian rainforest or vine thickets (Mackness unpub.). Fossils of short-necked chelids dominate the Bluff Downs fauna at the time of preservation, indicating a Pliocene palaeo-environment with well-developed rivers, creeks and lagoons and abundant aquatic fauna (Cann 1978; Legler 1985). The long-necked tortoises indicate that at the same time, there may have been shallow turbid lagoons (White 1997).

Chapter 5: A revision of the fossil Chelid turtles (Pleurodira) described by C.W. de Vis, 1897.

Published as: Thomson S. 2000. A Revision of the Fossil Chelid Turtles (Pleurodira)

Described by C.W. De Vis, 1897. *Memoires of the Queensland Museum* 45(2):593-598

Abstract

With increasing knowledge of the morphology of Australian chelid turtles and major changes in taxonomy it has become necessary to assign, where possible, the fossil species described last century by C.W. de Vis. It was found that four of these, *Chelymys uberrima*, *C. arata*, *C. antiqua* and *Pelecomastes ampla*, were synonymous, with *C. uberrima* being the senior synonym. *Chelymys uberrima* was determined to be a member of the *Elseya* whose affinities lie with the *Elseya lavarackorum* group of species. The paralectotypes of *Chelymys antiqua* were found to be a new species of the genus *Rheodytes* and sister to *R. leukops*. These specimens are described as a new species. *Chelodina insculpta* was found to be a valid taxon whose affinities probably lie with *C. expansa*.

Keywords: Testudines, side-necked turtle, Chelidae, Miocene, Pleistocene.

Introduction

The identification of fossil forms is an important addition to the understanding of the evolution and zoogeography of any species group. This is made difficult when the taxonomy of the extant forms is not well defined, as is the case for the Australian chelid turtles (Cogger et al., 1983; Thomson et al., 1997). With some recent advances on the skeletal morphology of chelids (Thomson & Georges, 1996; Thomson et al., 1997) it is now possible, and appropriate, to examine the fossil forms that have been described formally. For example, the recent description of a fossil turtle from Riversleigh, *Elseya lavarackorum* (White & Archer, 1994), and [its] subsequent discovery of a living population of this species (Thomson et al., 1997).

Fossil turtles in Australia have for many years been ignored due to the lack of detailed description of extant species. Rarely have skeletal diagnoses accompanied descriptions of the Australian chelid turtles, even those more recent. This makes the identification and placement of fossils difficult or impossible.

Apart from *Elseya lavarackorum* and *E. nadibajagu* Thomson & Mackness, 1999, only five other species of fossil chelid turtles have been described from Australia (Gaffney, 1981), all by C.W. de Vis (1897). Gaffney (1981) found that the available material was indeterminate below family or genus level was the last to revise the de Vis specimens. Three of the species, *Chelymys uberrima*, *C. antiqua* and *C. arata*, were identified as *Emydura* sp. (= *Emydura* + *Elseya* of Gaffney, 1977); another, *Chelodina insculpta*, was identified as *Chelodina* sp.; and the last, *Pelecomastes ampla*, could not be identified to family (Gaffney, 1981). These species were all described from fragmentary material from the Darling Downs with no holotypes identified (de Vis, 1897) hence Gaffney (1981) set lectotypes from each set of fragments and placed the rest of the specimens as syntypes. The specimens were originally diagnosed using differences in sulci (de Vis, 1897) but it seems that they were actually arranged according to scute ornamentation (Gaffney, 1981). This is a highly variable character and I agree with Gaffney (1981) that it is of little phylogenetic significance.

In this paper the fossil turtles described by de Vis (1897) are reanalyzed and, where appropriate, resurrected or placed in synonymy. They are placed in their correct genera using previously published diagnostic characters and their affinities and phylogenetic implications discussed. The purpose of this paper is to solve the nomenclatural problems associated with having described specimens of unknown affinity. It is not the purpose of this paper to present a review of the living genera with respect to the fossils.

Methods

Turtles representing all extant Australasian species have been borrowed from museums, collected or otherwise obtained, and skeletonized as per methods outlined in Thomson et al. (1997). This turtle collection of some 350 specimens is housed at the University of Canberra. Characters described in Thomson et al. (1997) were used for diagnosis and the fossils were then assigned to genus and their affinities demonstrated. A complete list of specimens examined can be found in Thomson et al. (1997). Further specimens with locality data will be presented in a future major analysis of the *Elseya* genus.

Systematics

***Elseya uberrima* (de Vis, 1897)**

Chelymys uberrima de Vis, 1897: 3.

Chelymys antiqua de Vis 1897: 4.

Chelymys arata de Vis 1897: 5.

Pelecomastes ampla de Vis 1897: 6-7.

Material: Holotype: none set (de Vis, 1897). Lectotype: QMF9040 by subsequent designation (Gaffney, 1981) (Fig. 1A). Paralectotypes: QMF1104, 1105 by subsequent designation (Gaffney, 1981). Lectotype of *Chelymys arata* QMF 16-1099B by subsequent designation (Gaffney, 1981) (Fig. 1 B). Lectotype of *Pelecomastes ampla* QMF1102D by subsequent designation (Gaffney, 1981) (Fig. 1C-D). Lectotype of *Chelymys antiqua* QMF 16-1106E by subsequent designation (Gaffney, 1981).

Horizon: Pliocene or Pleistocene.

Locality: Darling Downs, Queensland, Australia.

Discussion: Material consists of: QMF9040, nuchal, right peripherals 1-3, left and right pleural 1, articulated; QMF 11 04, numerous unarticulated carapace fragments including peripherals and pleurals; QMFI105, numerous unarticulated plastral fragments.

The lectotype assigned by Gaffney (1981) is suitably diagnostic and can be recognized as an *Elseya* without difficulty. The first vertebral scute is significantly wider than the second (Fig. 1A), a character found only in the *Elseya* and *Chelodina* (see Thomson et al., 1997). The *Chelodina* have either an anterior bridge strut restricted to the peripheral bones and not continuing on to the pleural bones, e.g. *C. longicollis* group except *C. novaeguineae* (see Thomson, [2000b]; Thomson et al., [2000]), or the strut continues on to the pleurals but not contributed to by the rib gomphosis, although it crosses it in some species, is wide throughout its length with a significant enlargement at the medial end, e.g. *C. expansa* group and *C. novaeguineae* (see Thomson, [2000b]; Thomson et al., [2000]). The structure of the anterior bridge struts in *Chelymys uberrima* is consistent with neither of the *Chelodina* conditions and is similar in structure to that described for the *Elseya lavarackorum* group (Thomson et al., 1997) (Fig. 2.). The structure of the first pleural and the indentation at the nuchal region places this species in the *Elseya lavarackorum* group of species. The fact that this species has a cervical scute is not unusual among fossil *Elseya*, particularly those from western flowing drainages.

Specimens in the South Australian Museum from Lake Palankarina and Lake Ngapakaldi all exhibit this feature and may represent an entire extinct radiation of *Elseya* turtles.

The four species synonymized above are, in this paper, recognized as a single diagnosable taxon, with *C. uberrima* being the senior-most available name (page priority). The genus *Chelymys* has been synonymized in recent years with *Emydura* (Cogger et al., 1983), the genus *Pelecomastes* is considered here a junior synonym of the genus *Elseya*, Gray 1867.

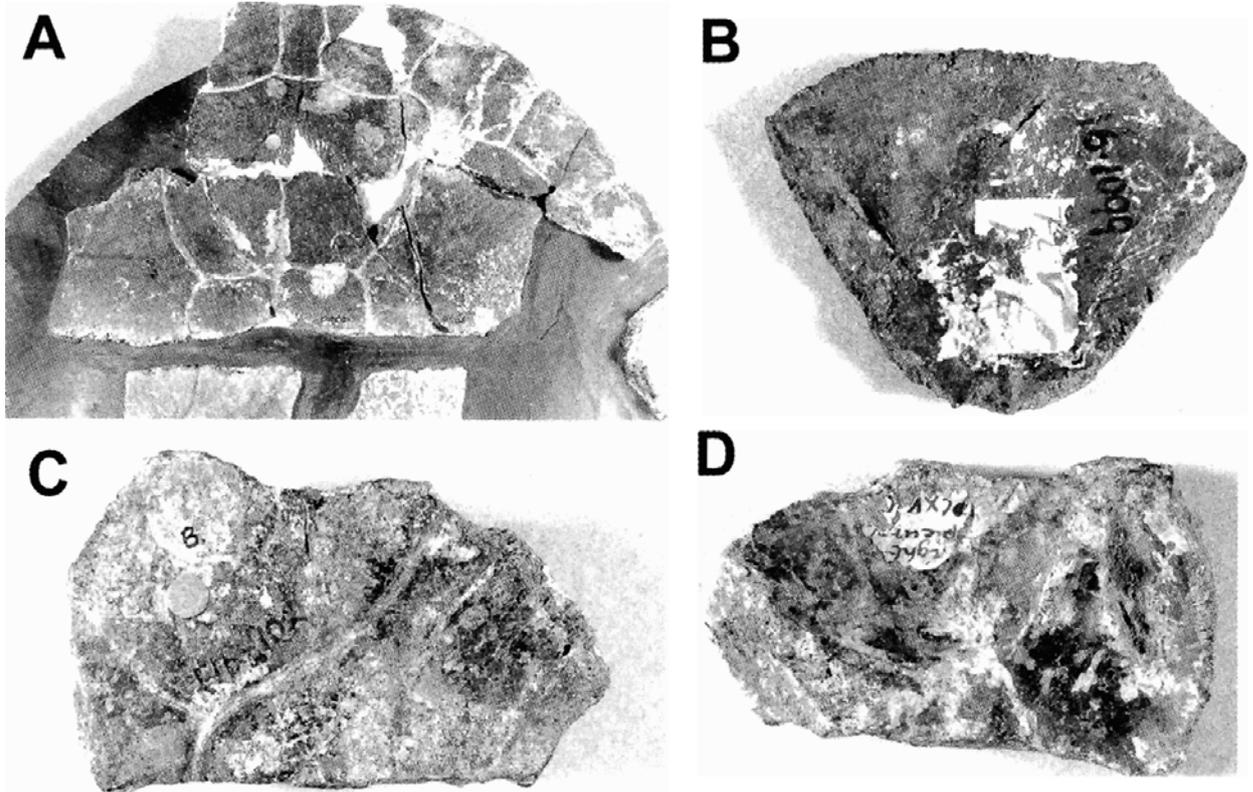


Figure. 1. A, Lectotype of *Elseya uberrima*, QMF9040, showing the enlarged first vertebral. B, Lectotype of *Elseya arata*, QMF16-1099B, now synonymized with *Elseya uberrima*. C-D, dorsal and ventral views of the Lectotype of *Pelecomastes ampla*, QMF1102D, now synonymized with *Elseya uberrima*; ventral view shows the large deviation of the anterior bridge strut from the rib/gomphosis.

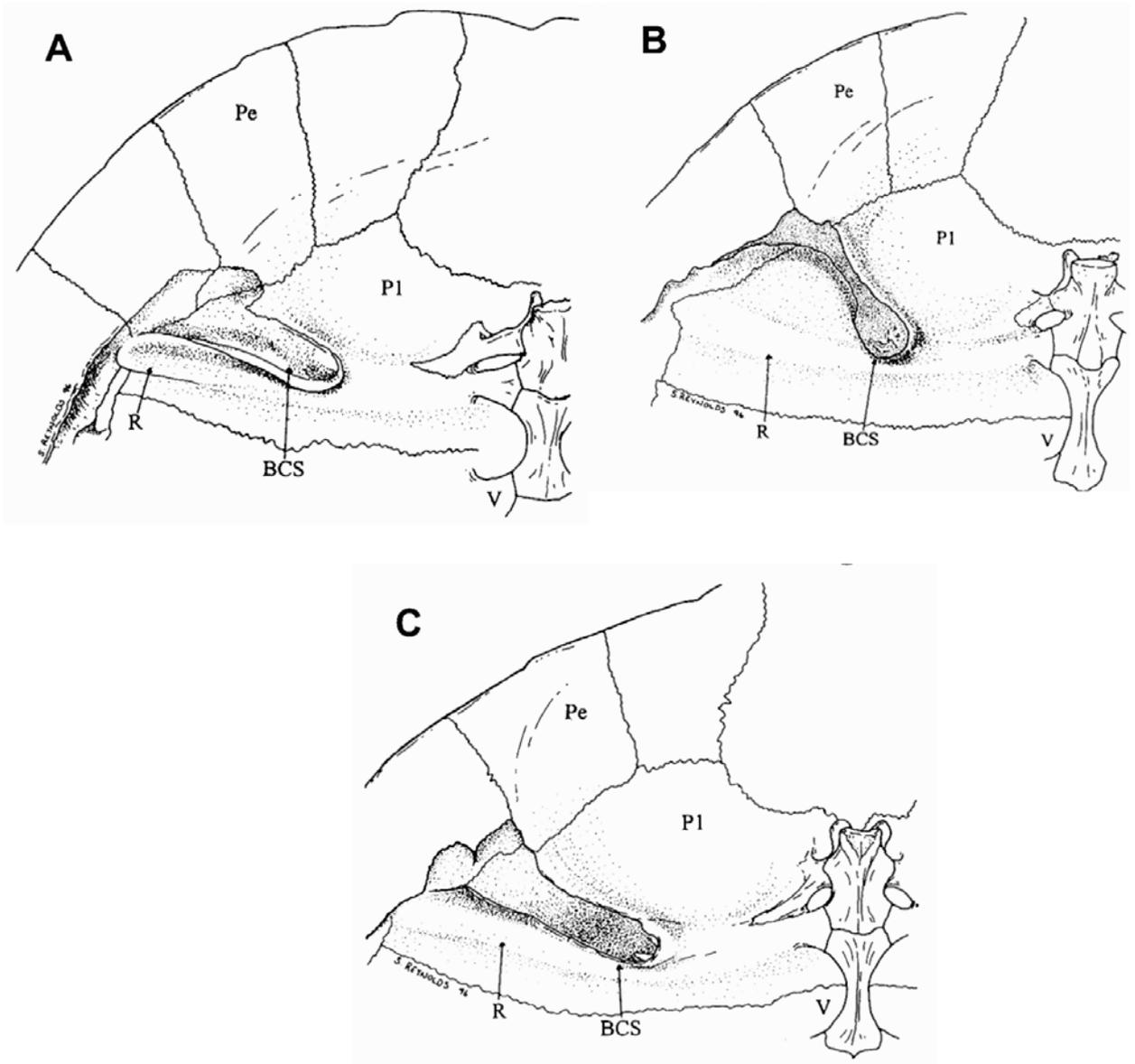


Figure. 2. Comparative diagrams of representative short-necked genera. A, *Elseya latisternum*; B, *Elseya dentata*; C, *Rheodytes leukops*; showing the angle between the rib/gomphosis (R) and the anterior bridge strut suture (BCS) on the first pleural (PI). (From Thomson et al., 1997).

These species were differentiated largely by shell ornamentation (Gaffney, 1981), an unsatisfactory method since this character can vary significantly even within a single population of turtles. The lectotype of *Chelymys antiqua* is not easily diagnosable. Based on the morphology of the pygal bone of extant species it would be attributed to almost any short-necked taxon in that the posterior suture of the ilium is in close proximity to the vertebral column. The *Elseya latisternum* group and *Pseudemydura* have a triangular suture on the pygal (unpublished data) ruling out these taxa. This pygal is either *Elseya* or *Emydura* but without the eighth pleural it is impossible to identify further (Thomson & Mackness, 1999). As there are no other diagnostic features between these specimens, all are considered as a single diagnosable taxon and assigned to *Elseya*.

Rheodytes devisi **sp. nov.**

Etymology: This species is named for C.W. de Vis who described most of the material presented in this paper as well as many other taxa within Australia

Material: Holotype: QMF16-1106B (Fig. 3A-B). Paratypes: QMF16-1106A, C-D.

Horizon: Pliocene or Pleistocene.

Locality: Darling Downs, Queensland, Australia.

Diagnosis: The genus *Rheodytes* can be diagnosed by the presence of a 10-15° angle between the anterior bridge strut and the rib/gomphosis of pleural one, and by the parallel sutural edges of the bridge strut with intervening deep socket like sutural surface (Thomson et al., 1997) (Fig. 2C). This combination of characters is unique to this genus and is present in both specimens of first pleurals in the type series (Fig. 3B-C). The species *Rheodytes devisi* is diagnosed by its thicker, better formed, carapacial bones. Deeper insertion of the anterior bridge strut suture and the failure of the anterior bridge strut to either break through, or come close to breaking through, the pleural surface.

Discussion: Material consists of: QMF16-1106B, right first pleural, almost complete (Fig. 3A-B); QMF16-1106C, distal section of a right first pleural (Fig. 3C); QMF 16-1106D, left partial pleural of indeterminate position but likely from the seventh pleural.

Rheodytes leukops is an inhabitant of the Fitzroy River in eastern Queensland, whereas *R. devisi* is found in the western flowing drainages of the Darling Downs. Among the extant taxa *Rheodytes leukops* can be identified by its extremely thin shell, to the point that the ilium and bridge strut often break through the carapace, all other genera have thicker shells ranging from the *Elseya latisternum* group through to the *Emydura* and *Elseya* groups. *R. devisi* has a thick shell much like other short-necked

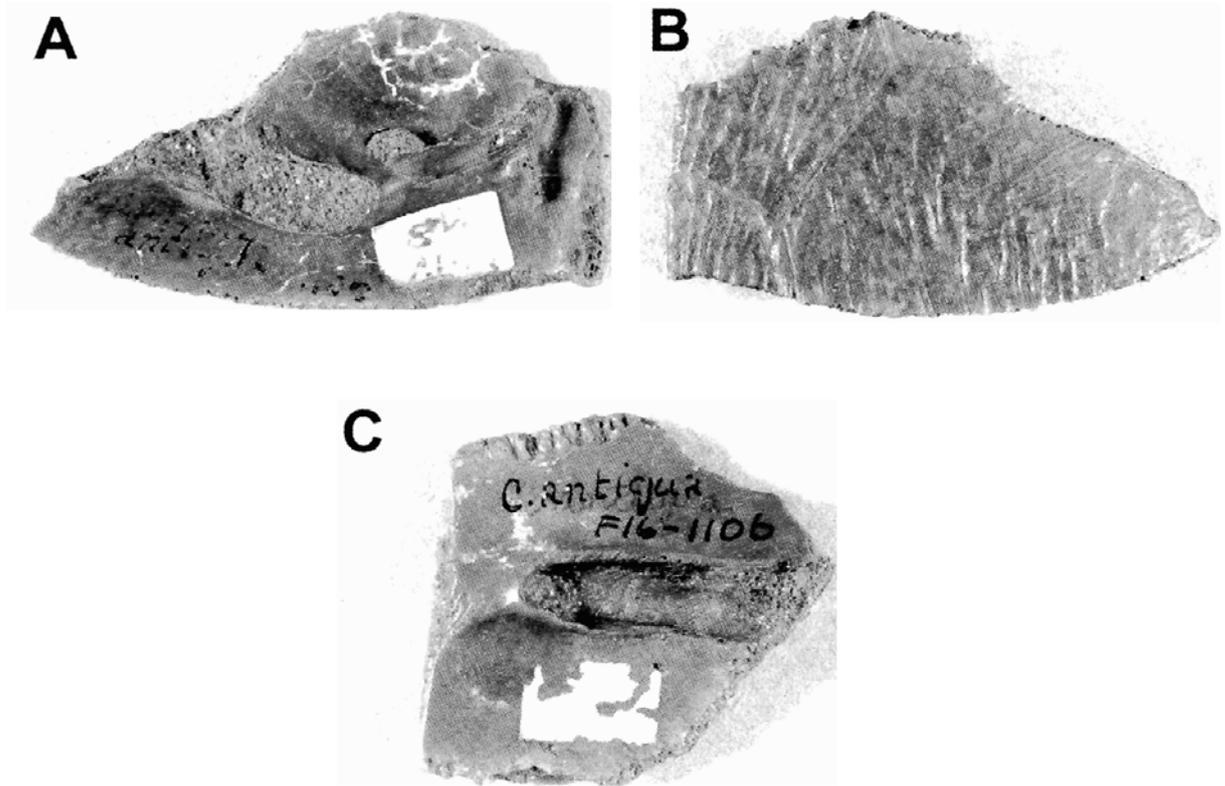


Figure. 3. Ventral and dorsal views of *Rheodytes devisi*, the ventral views showing parallel sutural edges and low angle of the anterior bridge strut. A-B, Holotype, QMF16-1106B; C, Paratype QMF 16- 1 106C.

species and hence it can be diagnosed from its congener *R. leukops*. The species are allochronic and allopatric and appear to have inhabited different environments.

***Chelodina insculpta* de Vis, 1897**

Chelodina insculpta de Vis, 1897.

Material: Holotype: none set (de Vis, 1897). Lectotype: QMF1109A by subsequent designation (Gaffney, 1981) (Fig. 4). Paralectotypes: QMF 16- 1 107, F 1 109B-G by subsequent designation (Gaffney, 1981).

Horizon: Pliocene or Pleistocene.

Locality: Darling Downs, Queensland, Australia, restricted (this study).

Discussion: Material consists of: QMF 16- 1 107 (fig. V in de Vis, 1897), numerous carapace fragments including parts of pleurals and peripherals. Most of these are not particularly diagnostic. There is a partial articulated 6th and 7th pleural from the left side that has characters diagnostic of *Chelodina*. The fragment listed as D in de Vis' figure V is actually a 7th pleural not a 6th. QMF1109a-g (fig. VI in de Vis, 1897), various plastral units which can clearly be diagnosed as *Chelodina* using the lectotype, QMF 1 109A (Gaffney, 1981). This would appear, however, to represent at least two animals as sutural surfaces are preserved yet there is no match between the anterior and posterior halves of the plastron.

The material available is diagnosable to genus using the scute sulci arrangements of the lectotype, an entoplastron in which there is clearly a large intergular which is separated from the margin anteriorly by the gulars a unique feature of the *Chelodina* (Gaffney, 1981) (Fig. 5). There is further evidence of generic assignment from the relative widths of the anterior and posterior parts of the posterior lobe of the plastron and from the positioning of the pelvic suture on pleural seven of the carapace.

Chelodina insculpta possessed a large, robust bridge strut, a character unique to the *C. expansa* group of species (Thomson, [2000]; Thomson et al., [2000]). Further, this specimen had a large carapace excluding many species from the *C. expansa* group, such as *C. rugosa*, which have a reduced margin. However, the margin is not as flared at the posterior or as wide as *C. expansa*. Therefore, *C. insculpta* is recognized as a valid taxon.

The locality data for this species was originally given as a combination of the Darling Downs, Queensland; Warburton River, South Australia; and Eight Mile Plains near Brisbane. Queensland (de Vis, 1897). In the original description de Vis states that the Warburton material was not figured and consisted of seven carapace fragments. As the name bearing

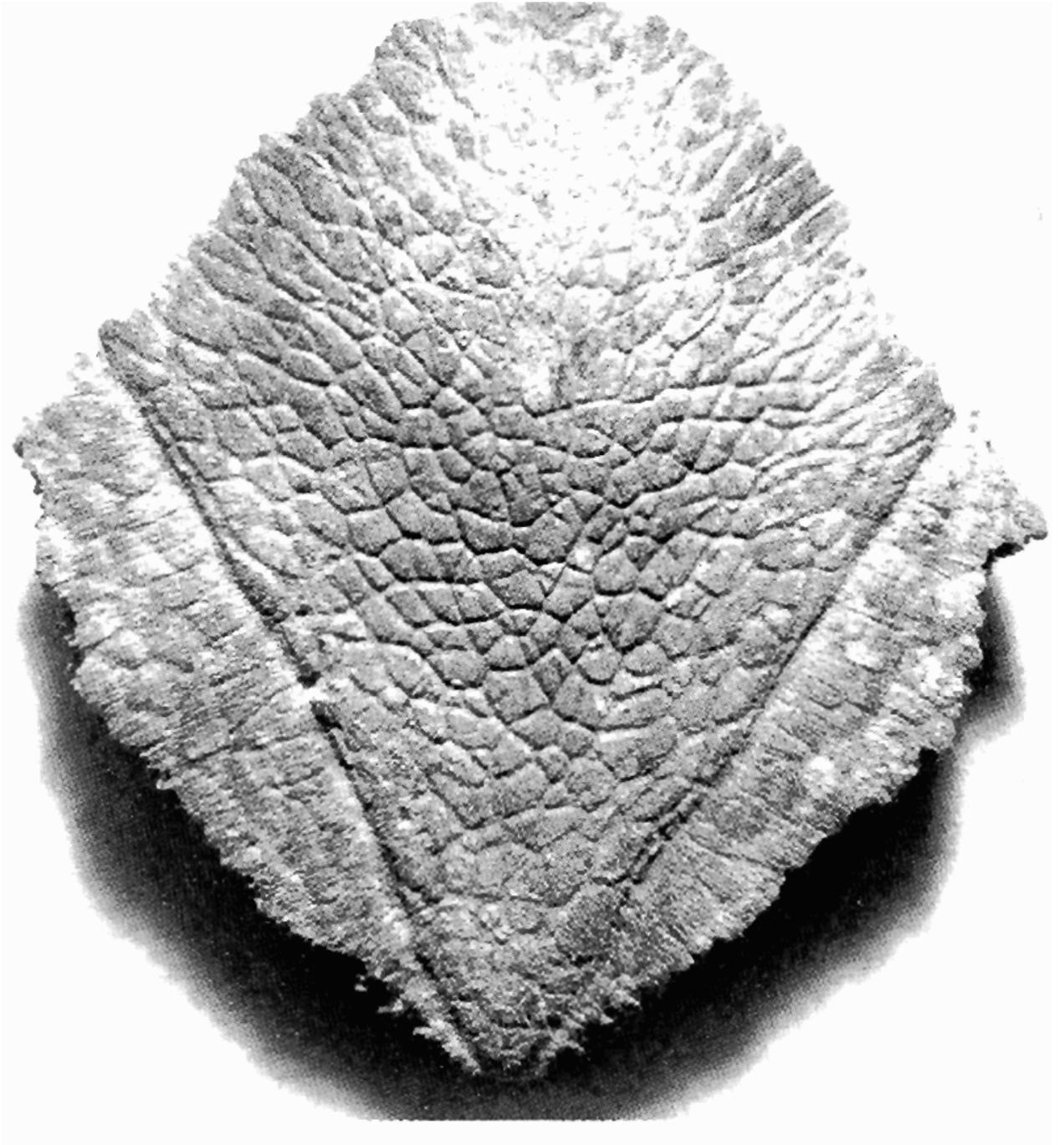


Figure. 4. Ventral view of Lectotype of *Chelodina insculpta*, QMF1109A, showing large area of the intergular scute on this unit.

lectotype is an entoplastron this rules out the Warburton River as a type locality. There is no mention of Eight Mile Plains until the locality section of the paper and de Vis clearly states that 'in addition to the fragments of carapace figured, sixteen others from the Darling Downs. It seems clear that despite other material examined only Darling Downs material was figured. As the lectotype (QMF1109a) is clearly identifiable in figure VI of de Vis (1897) I am restricting the type locality to the Darling Downs of Queensland.

Discussion

The five species and one genus described by de Vis (1897) are reduced to three species and *Chelymys* and *Pelecomastes* are synonymized with *Elseya*. *Elseya uberrima* is an extinct form of snapping turtle belonging to a large group that possibly contains the New Guinea forms as their sole surviving relatives. They would appear to be the sister group of the *Elseya lavarackorum* group (*sensu* Thomson et al., 1997). *Rheodytes devisi* is the first fossil record of this highly restricted genus of turtles. Clearly sister taxa, they were found on opposing sides of the Great Dividing Range. *Chelodina insculpta* is a large long neck turtle from an area where *C. expansa* may still be found. This species would appear to be part way between the body forms associated with *C. expansa* and *C. rugosa*, and likely to be the sister species of *C. expansa*.

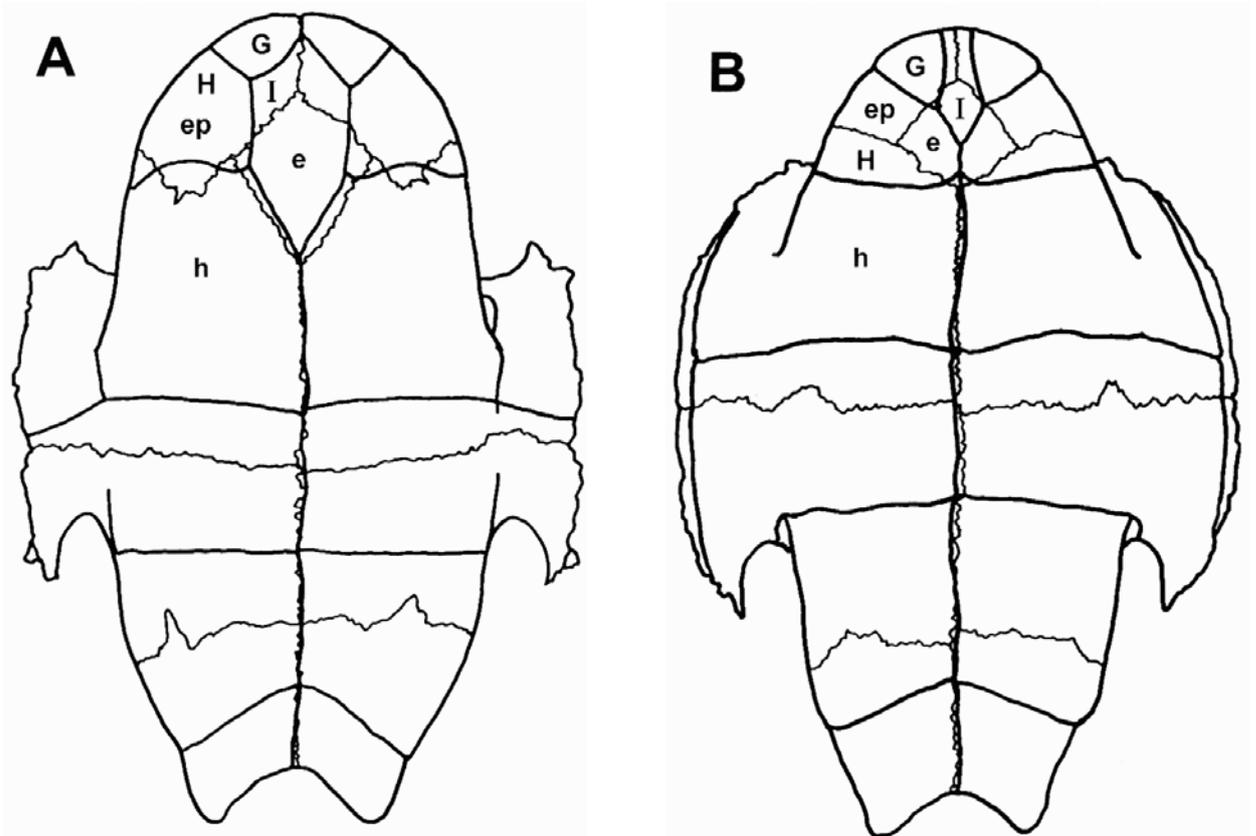


Figure. 5, Comparisons of the intergular region of A, *Chelodina rugosa* and B, *Elseya dentata*; showing difference between the *Chelodina* and Short-necked conditions.

Chapter 6: A New Species of Freshwater Turtle in the Genus *Elseya* (Testudines: Chelidae) from Central Coastal Queensland, Australia.

Published as: Thomson, S., Georges, A. & Limpus, C. 2006. A New Species of Freshwater Turtle in the Genus *Elseya* (Testudines: Chelidae) from Central Coastal Queensland, Australia. *Chelonian Conservation and Biology* 5: 74-86.

Abstract

In this paper, we describe a new species of freshwater turtle from the Burnett River of coastal Queensland. It is a large, predominantly herbivorous species previously regarded to belong to the widespread species *Elseya dentata*. It is most closely related to *Elseya irwini*, *E. lavarackorum*, an undescribed taxon from the Johnstone River of northern Queensland, and possibly *E. branderhorsti* from New Guinea. It can be distinguished from the above species by the combination of a robust skull that acutely narrows across the *pterygoids* behind the *processus pterygoideus externus*, a deeply furrowed head shield and underlying bone, very prominent alveolar and lingual ridges on the triturating surfaces, a serrated margin to the carapace (prominent in juveniles and persisting into early adulthood), an anterior plastron that is broad, not oval in outline, and notable irregular white or cream markings on the lateral and ventral surfaces of the head and neck of adult females, often extending down the forelimbs. The new species inhabits the coastal Mary, Burnett, Fitzroy-Dawson, and associated smaller drainages of southeastern Queensland.

Keywords: Reptilia; Testudines; Chelidae; *Elseya* sp. nov.; turtle; side-neck turtle; taxonomy; systematics; Pleurodira; Australia

Introduction

The freshwater turtle fauna of the Australasian region is dominated by a single family, Chelidae, found elsewhere only in South America. The taxonomy of Australasian chelids is poorly known, and many species have only recently been described. Those described in the last decade include *Chelodina pritchardi* (Rhodin 1994a) from New Guinea, *C. mccordi* (Rhodin 1994b) from the island of Roti in Indonesia, *C. burrungandjii* (Thomson et al. 2000) from Arnhem Land, *Elusor macrurus* (Cann and Legler 1994) from the Mary River in southeastern Queensland, *Elseya lavarackorum* (White and Archer 1994) first described as a fossil specimen from Riversleigh in Queensland but later established as extant (Thomson et al. 1997), *Elseya irwini* (Cann 1997b) from northeastern Queensland, *Elseya georgesi* (Cann

1997a) from coastal New South Wales and *Emydura tanybaraga* (Cann 1997c) from northern Australia. Several new fossil taxa have been described, including *Elseya nadibajagu* (Thomson and Mackness 1999), *Birlimarr gaffneyi* (Megirian and Murray 1999), *Rheodytes devisi* (Thomson 2000a), and *Chelodina alanrixi* (Lapparent de Broin and Molnar 2001).

Recent surveys using allozyme electrophoresis (Georges and Adams 1992, 1996; Georges et al. 2002) have established that many more extant species await description. Species of the genus *Elseya* fall into two distinct clades that are in a paraphyletic arrangement, their common ancestor having *Emydura* among its descendants (Georges and Adams 1992). The first of these clades is referred to as the *E. latisternum* generic group and comprises *E. latisternum*, *E. georgesi*, *E. purvisi*, and *E. belli*, with the second clade referred to as the *E. dentata* generic group and comprises the type species for the genus *E. dentata*, together with *E. branderhorsti*, *E. novaeguineae*, *E. schultzei*, *E. irwini*, and *E. lavarackorum* (Georges and Adams 1992; Thomson et al. 1997). To resolve this paraphyly, it is anticipated that these two generic groups will one day be recognized as separate genera.

The *E. dentata* generic group, characterized by the presence of an alveolar ridge on the triturating surfaces of the jaw, contains large river turtles distributed from the Mary River of southeastern Queensland to the Fitzroy River of northern Western Australia. The Australian forms were once regarded as a single widespread species, *E. dentata*, but electrophoresis revealed a series of highly divergent allopatric forms. Each was regarded by Georges and Adams (1996) as a distinct species. In this paper, we provide a formal description for one of these species from the rivers of central coastal Queensland (Fig. 1).

Methods

We examined all available specimens of *Elseya* from the Australian Museum (AM), the Museums and Art Galleries of the Northern Territory (NTM), The Queensland Museum (QM), the Western Australian Museum (WAM), the National Wildlife Collection (ANWC), and the Natural History Museum of London (NHM). Additional specimens in the collection of J.M. Legler at the University of Utah (UU) and the senior author (UC) were also examined as part of the study. Specimens examined are listed in Appendix B. Names of skull elements follows that of Gaffney (1979); shell terminology follows that of Zangerl (1969) with modifications for costals suggested by Pritchard and Trebbau (1984). Bridge strut terminology follows that of Thomson et al. (1997) and Thomson and Mackness (1999).



Figure 1. A female *Elseya albagula* from the Burnett River showing the prominent light markings on the lateral and ventral surfaces of the head and neck. The male (inset top left) is from Barambah Creek, Burnett River, and the juvenile (inset top right) is from the Mary River, near Kenilworth. Note the prominent serrations on the shell of the juvenile. Photos by John Cann.

Systematics

Order: Testudines Linnaeus, 1758

Suborder: Pleurodira Cope, 1864

Family: Chelidae Gray, 1831

Elseya albagula, sp. nov.

Southern Snapping Turtle (Fig. 2, Table 1)

Type Specimens. — Holotype: QM J81785, adult female collected by Duncan Limpus on 24 October 2004 from the plunge pool at the downstream side of the Ned Churchwood Weir, Burnett River, Queensland, Australia (25°03'S, 152°05'E) (Fig. 2). Allotype: QM 28449, adult male from Nogoia River, Fitzroy River Drainage, Queensland (23°31'S, 148°01'E) (Fig. 3). Paratypes: QM 37933, adult male from Dawson River Crossing at Baroondah Station, Fitzroy River Drainage, Queensland (25°41'S, 149°13'E); QM 36041, 36044, two juveniles from Coondoo Creek, Tin Can Bay Road, Mary River Drainage, Queensland (25°59'S, 152°05'E). See Tables 2 and 3 for comparative measurements.

Referred Specimens. — QM 2966, 4501, 4505, 36036, 36039, 36042, 36045–7, 38533, 47987, 47998, 48002, 48010, 48012, 48026–27, 48029, 48039, 48046, 48052, 59269–71; UC 0305–6; UU 17086–102, 17274, 17874–903, 18514.

Diagnosis. — The largest extant species of *Elseya*, reaching carapace lengths of 420 mm. Belongs to the *E. dentata* generic group, and as such can be distinguished from all members of the *E. latisternum* generic group by the following combination of characters: parietal arch narrow, much narrower than the otic chamber; head shield does not extend from the dorsal surface of the skull down the parietal arch toward the tympanum; alveolar ridge present on the triturating surfaces of the mouth; intergular scute narrow, maximum width less than that of the gulars.

Elseya albagula can be distinguished from species within the *E. dentata* generic group by the following combination of characters: skull robust but narrows acutely across the *pterygoids* behind the *processus pterygoideus externus* (Fig. 4); head shield deeply furrowed to the extent that osteologically there are also deep furrows in the dorsal surface of the skull of large adults; alveolar ridge on the triturating surfaces and underlying bone of the upper jaw very prominent, forming a complex with the equally prominent lingual ridge (Fig. 4). This complex corresponds with prominent ridges and cavities in the lower jaw to form shearing surfaces; lingual ridge of maxilla expanded such that, in older specimens, it obscures the *foramen praepalatinum* in ventral view.

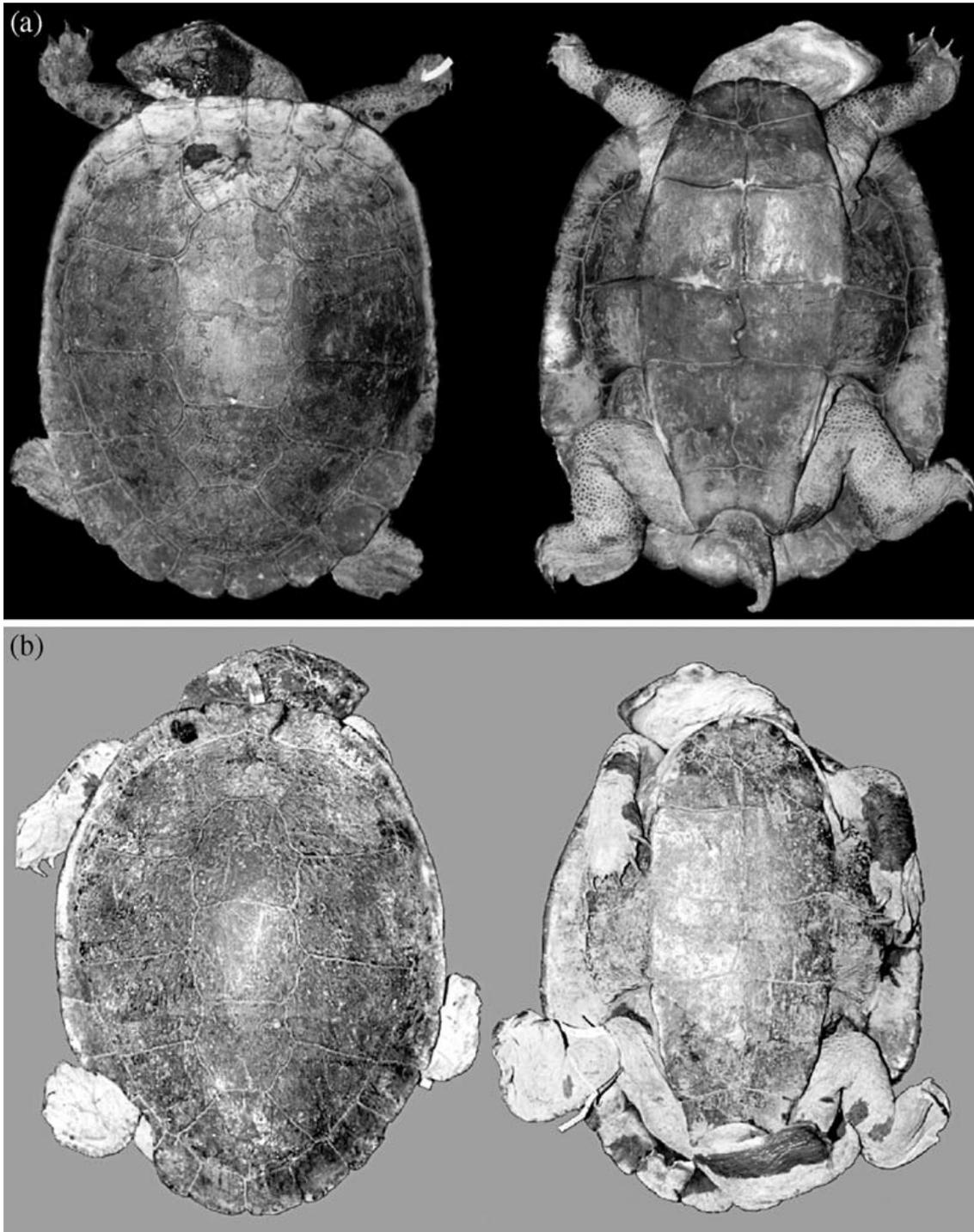


Figure 2. *Eseya albagula* type specimens: (a) the female holotype (Queensland Museum [QM] J81785, carapace length [CL] = 382.4 mm) photographed alive and (b) the male allotype (QM J28449, CL = 275.5 mm), spirit preserved.

Table 1. Measurements of the type specimens.¹

Mus. No.	Status	Sex	HL	HW	PW	IO	OD	CL	CW4	CW8	V1	V2	PL
QM J81785	Holotype	Fem	96.10	69.22	41.25	19.12	15.92	382.40	263.73	299.33	87.92	80.90	315.40
QM 28449	Allotype	Male	67.52	53.08	27.18	14.82	12.25	275.49	182.7	214.77	54.73	59.83	224.87
QM 37933	Paratype	Male	65.28	49.13	26.23	18.35	12.37	261.55	179.2	204.42	59.82	57.84	218.56
QM 36041	Paratype	Juv	37.59	26.48	17.04	6.8	8.45	144.35	97.76	130.18	33.72	46.52	109.73
QM 36044	Paratype	Juv	23.54	17.6	11.65	4.01	6.62	91.89	73.02	93.88	24.32	34.36	68.34

1. QM, Queensland Museum; HL, head length; HW, head width at tympanum; PW, parietal width; IO, interocular width; OD, ocular diameter; CL, carapace length; CW4, carapace width 4; CW8, carapace width 8; V1, width of vertebral 1; V2, width of vertebral 2; PL, plastron length (see Appendix A).

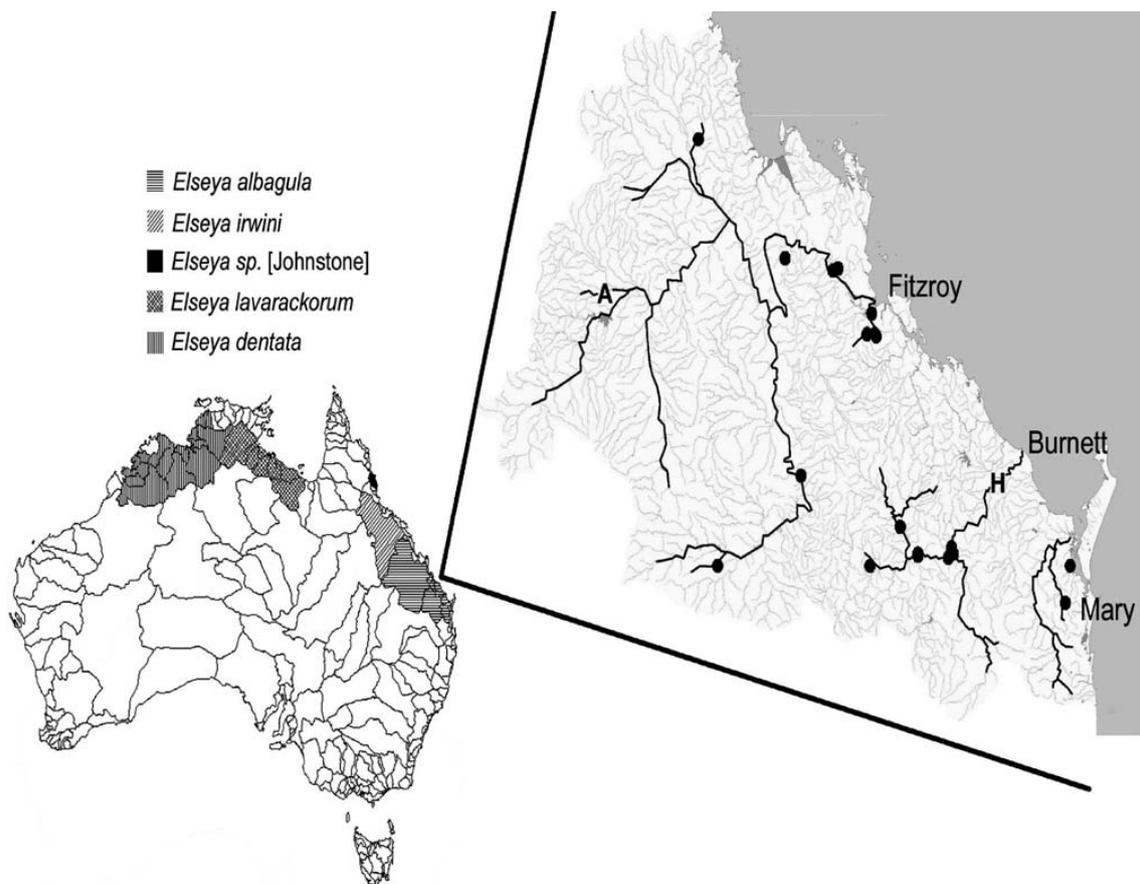


Figure 3. Distribution of species of the *Elseya dentata* subgeneric group in Australia: generalized watershed distributions of *E. dentata* (sensu stricto), *E. lavarackorum*, and *E. irwini* are shown, with specific localities for *E. albagula* (d). An undescribed form (not shown) occurs also in Arnhem Land.

Anterior carapace blunt, with the first and second marginal scutes approximately equal in their anterior extent in large individuals (Fig. 5); carapace with serrated margin, most prominent in juveniles where serrations begin at the posterior edge of marginal 1 (Fig. 5); serrated margin persists into early adulthood; cervical scute absent (Fig. 5), except as a rare variant; anterior plastron broad, not oval in outline; posterior bridge strut articulates with the carapace posterior to the midline of pleural 5 or on the junction of pleurals 5 and 6, rarely on pleural 6 alone.

Distribution. — The major drainage basins of the Fitzroy, Burnett, and Mary rivers of southeast Queensland, Australia (Fig. 3), with records also from the minor Raglan, Kolan, and Gregory-Burrum drainages. Occurs in sympatry with *Elseya latisternum*, *Chelodina longicollis*, *C. expansa*, and *Emydura macquarii krefftii* in all three drainages that comprise its range; also with *Elusor macrurus* in the Mary River and *Rheodytes leukops* in the Fitzroy drainage.

Etymology. — The name *albagula* is derived from the Latin adjective “*alba*” meaning white (feminine) and the noun “*gula*” for throat, which is also feminine. Hence the name means “white throat,” and refers to the white or cream throat commonly seen in adult females of this species.

Related Taxa. — The affinities of *E. albagula* lie with a well-defined clade within the *E. dentata* subgeneric group comprising *E. irwini*, *E. lavarackorum*, an undescribed taxon from the Johnstone Rivers region of north coastal Queensland (Georges and Adams 1996), and possibly New Guinean *E. branderhorsti* (Thomson, unpub. data, 1996), but excluding *E. dentata*, *E. novaequinae*, *E. schultzei*, an undescribed taxon from Arnhem Land, and a number of other undescribed species from the New Guinea region. We consider the closest living relative to be an undescribed taxon from the Johnstone Rivers region near Cairns, but among described taxa, it is *E. lavarackorum* (White and Archer 1994) from the Nicholson Drainage, Queensland, not *E. irwini* (Cann 1998) from the Burdekin River, Queensland.

Description

External Morphology

Carapace. — Carapace broadly oval posteriorly, blunt anteriorly (Fig. 5). Marginals 2–6 upturned and marginals 7–11 expanded and flared laterally in adults. Adult carapace is dark brown to black in color, often also heavily stained. Surface smooth, with or without growth rings, and lacks luster.

Table 2. Relative measurements of the head for *Elseya*.¹

Species	Sex	Size	HL	HW/HL	PW/HL	IO/HL	OD/HL	HL/CL
<i>E. albagula</i>	Unsexed	0–200	38.3 ±9.1 (9)	69.8 ± 2.5 (9)	45.4 ± 2.5 (9)	17.5 ± 1.0 (9)	22.5 ± 2.3 (9)	25.7 ± 0.7 (9)
		200–250	57.7 ± 0.7 (2)	69.5 ± 1.9 (2)	39.5 ± 0.2 (2)	18.6 ± 0.6 (2)	19.8 ± 0.4 (2)	24.5 ± 1.6 (2)
	Female	250–300	64.1 ± 3.2 (5)	74.1 ± 4.1 (4)	40.6 ± 2.4 (5)	22.8 ± 3.2 (5)	18.6 ± 0.7 (5)	24.0 ± 0.8 (5)
		200–250	56.0 ± 1.6 (3)	65.8 ± 1.5 (3)	40.1 ± 1.7 (3)	17.7 ± 0.6 (3)	19.1 ± 0.6 (3)	25.7 ± 0.5 (3)
		250–300	70.1 (1)	70.4 (1)	44.1 (1)	22.8 (1)	17.7 (1)	25.9 (1)
		>300	84.8 ± 8.7 (4)	75.3 ± 0.0 (4)	41 ± 0.0 (4)	20.6 ± 0.0 (4)	19.3 ± 0.0 (4)	22 ± 0.0 (4)
		Unsexed	0–200	27.5 (1)	—	46.9 (1)	15.8 (1)	26.7 (1)
	Male	200–250	52.9 ± 2.0 (8)	65.1 ± 2.5 (8)	42.6 ± 2.0 (8)	19.5 ± 1.1 (8)	21 ± 0.7 (8)	24.5 ± 0.7 (8)
		250–300	57.9 (1)	76.7 (1)	41.1 (1)	23.2 (1)	20.4 (1)	22.1 (1)
Female	250–300	64.9 (1)	73.0 (1)	49.7 (1)	20.9 (1)	20.1 (1)	24.3 (1)	
	>300	78.8 ± 3.0 (2)	70.1 ± 6.5 (2)	44 ± 1.6 (2)	20.3 ± 3.2 (2)	19.5 ± 0.6 (2)	24.3 ± 1.4 (2)	
<i>E. lavarackorum</i>	Unsexed	0–200	37.2 ± 7.2 (7)	69.2 ± 2.0 (7)	42.8 ± 2.3 (7)	18.2 ± 1.3 (7)	22.1 ± 2.0 (7)	24.0 ± 2.1 (7)
		200–250	49.3 ± 1.0 (3)	66.4 ± 1.8 (3)	40.6 ± 3.0 (3)	17.8 ± 1.2 (3)	20.7 ± 1.1 (3)	23.4 ± 0.6 (3)
	Female	200–250	50.8 ± 0.3 (2)	68.8 ± 5.0 (2)	41.7 ± 0.7 (2)	18.0 ± 1.6 (2)	19.6 ± 0.2 (2)	24.2 ± 1.4 (2)
		250–300	72.0 ± 2.7 (2)	69.9 ± 4.6 (2)	40.2 ± 2.9 (2)	17.3 ± 1.2 (2)	20.0 ± 1.4 (2)	23.2 ± 0.1 (2)
	Unsexed	0–200	32.2 ± 4.9 (2)	71.9 ± 0.7 (2)	45.2 ± 1.2 (2)	14.3 ± 5.5 (2)	22.2 ± 2.6 (2)	27.0 ± 1.1 (2)
		Female	250–300	79.9 ± 1.5 (2)	70.1 ± 2.2 (2)	41.4 ± 1.5 (2)	18.9 ± 1.0 (2)	16.5 ± 2.8 (2)
<i>E. dentata</i>	Unsexed	0–200	42.8 ± 5.8 (7)	69.9 ± 5.1 (7)	42.3 ± 4.7 (7)	18.6 ± 1.3 (7)	20.8 ± 2.9 (7)	25.4 ± 2.0 (7)
		200–250	59.0 ± 1.5 (6)	70.7 ± 2.7 (6)	42.1 ± 0.5 (6)	21.0 ± 1.7 (6)	19.4 ± 0.7 (6)	24.7 ± 1.2 (6)
	Male	250–300	61.9 ± 4.7 (8)	73.2 ± 4.1 (8)	40.2 ± 3.7 (8)	19.8 ± 1.5 (8)	20.6 ± 1.5 (8)	23.1 ± 1.4 (8)
		200–250	50.1 (1)	70.0 (1)	42.6 (1)	19.8 (1)	19.6 (1)	25.1 (1)
	Female	250–300	65.8 ± 5.2 (10)	72.4 ± 4.0 (10)	39.9 ± 4.0 (9)	20.5 ± 1.4 (10)	20.3 ± 2.2 (10)	23.6 ± 2.1 (10)
		>300	61.3 ± 14.7 (2)	73.2 ± 1.9 (2)	41.4 ± 2.4 (2)	20.8 ± 1.2 (2)	21.1 ± 2.2 (2)	19.7 ± 5.7 (2)

1. Abbreviations as per Appendix A. Means are given with standard deviations and sample sizes. Non-ratio measurements and ranges in mm.

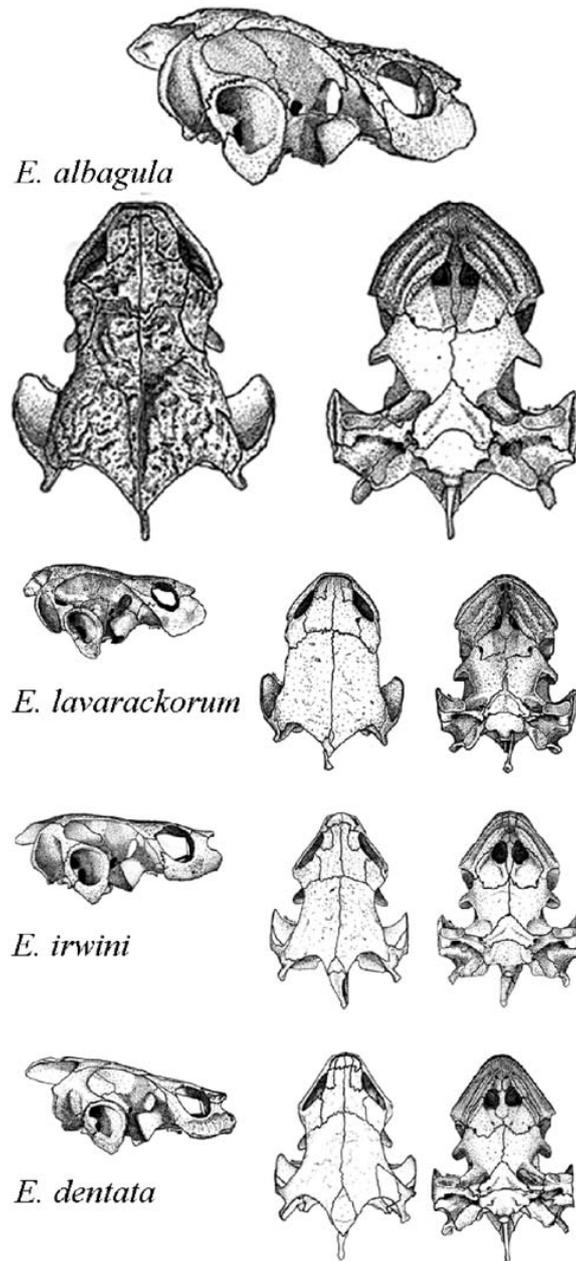


Figure 4. Lateral dorsal and ventral views of the skull of *Elseya albagula* (Queensland Museum [QM] 59270, head length [HL]= 75.7 mm); *Elseya lavarackorum* (QM 46284, HL = 81.4 mm); *Elseya irwini* (National Wildlife Collection 0520, HL = 69.6 mm); *Elseya dentata* (QM 59277, HL = 63.8 mm).

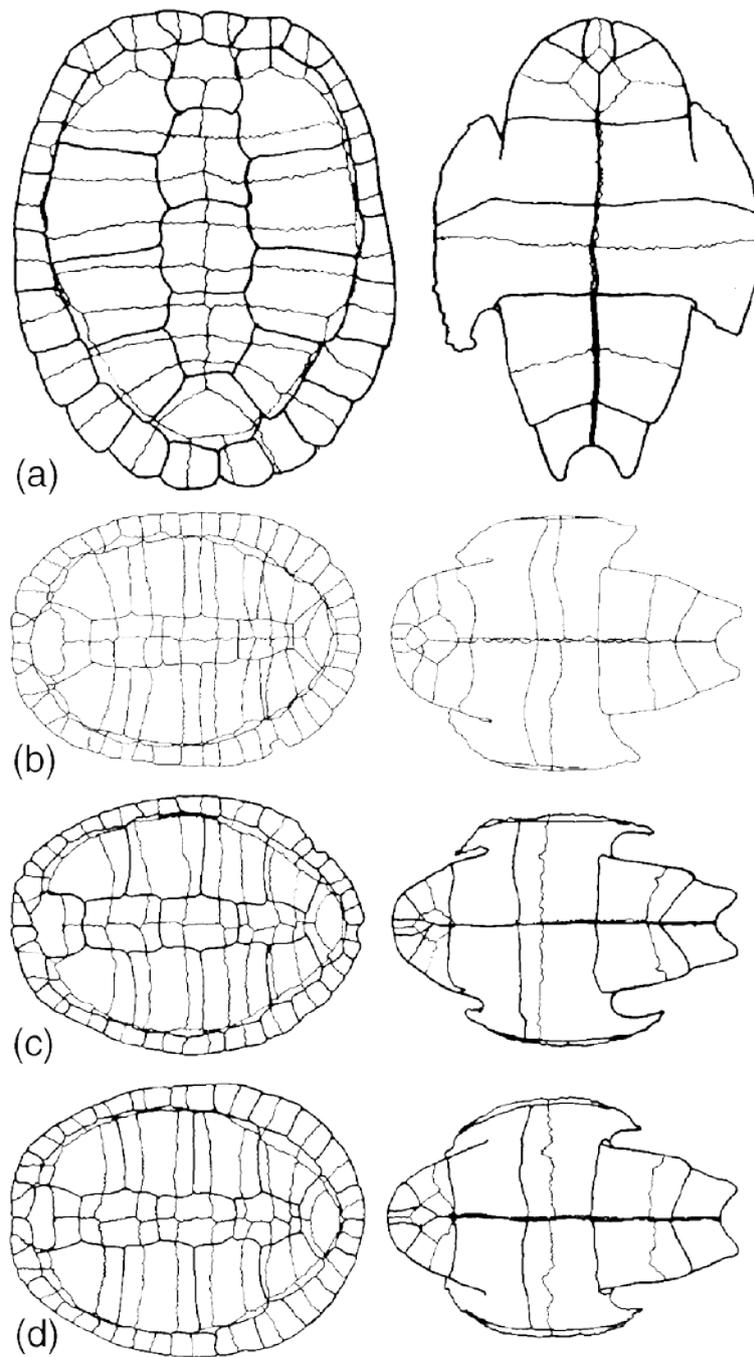


Figure 5. Dorsal view of the carapace and ventral view of the plastron for (a) *Elseya albagula* (Queensland Museum [QM] 59270, carapace length [CL] = 377.5 mm); (b) *Elseya lavarackorum* (QM 46284, plastron length = 275.5 mm); (c) *Elseya irwini* (National Wildlife Collection 0520, CL = 281.2 mm); and (d) *Elseya dentata* (QM 59277, CL = 293.5 mm).

Medial keels distinct on all vertebral and costal scutes of juveniles, forming a tricarinate ridged carapace; keels indistinct or absent in adults. Carapace of juveniles serrated from the posterior edge of marginals 1 (Fig. 6); young adults have a serrated margin from marginals 7. Spiny protrusions on the ends of marginals (Fig. 1) present to ca. 120 mm carapace length. These features are thought to derive from very rapid growth, and combine to make a very distinctive juvenile. Juvenile carapace tan, mottled with dull brown to black in small juveniles, changing to dark brown or black at variable size (in one case as small as 71 mm CL). Irregular mottling on each scute, concentrated as ragged blotches on and straddling the sulci.

Plastron. — Plastral formula (using midline length) of the holotype: fem . pec . abd . int . ana _ gul (Fig. 5), with no variation among the adult plastra examined. Plastron narrow with axillary width ca. 50% of carapace width. Base of anterior lobe does not taper, its lateral margins roughly parallel for the length of the pectoral. Bridge extensive and posterior lobe longer than anterior lobe. Color of adult plastron often difficult to determine because of complete staining to black, but base color cream to yellow, with or without darker streaks and blotches. Axillary and inguinal scutes present.

Plastron yellow, mottled with indistinct black or brown, in some cases yielding a radial pattern in the direction of scute growth. Mottling concentrated on bridge and posterior half of the plastral surface. Inframarginal surfaces similarly mottled with irregular brown. Pale fields on inframarginals tinged with pinkish orange. Pattern becomes indistinct and inframarginal surfaces lose pale fields even in juveniles as small as 100 mm.

Head and Soft Parts. — Head large, robust, but not to the extent of its nearest relatives within the *E. lavarackorum* group; dark brown above, cream, yellow, or white below in females; typically grey but occasionally cream below in males. Boundary between light ventral coloration and darker dorsal coloration of head and neck very irregular, forming large, distinctive patches that vary with age and among individuals (Fig. 7).

Tomial sheath of upper jaw yellow, cream, or grey, sometimes with vertical barring (Fig. 7). Head shield entire, extending from immediately posterior to the nasals, over the parietal to the posterior extent of the skull; deeply furrowed, involving both scutes and the bone beneath in large adults. Head shield does not extend laterally to contact or approach the tympanum. Temporal region covered in medium rounded hard scales. Two very prominent barbels on chin, rounded (not pointed) terminally;

Table 3. Relative measurements of the carapace and plastron for *Elseya*.¹

Species	Sex	Size	CL	HL/CL	CW4/CL	CW8/CL	V1/CL	V2/CL	PL/CL	
<i>E. albagula</i>	Unsexed	0–200	149.4	25.7	69.1	87.6	24.7	32.9	76.9	
			± 36.5 (9)	±0.7 (9)	±5.1 (9)	±6.6 (9)	±1.2 (9)	±2.8 (9)	±2.0 (9)	
	Male	200–250	236.6	24.5	71.1	72.1	22.9	23.4	79.8	
			± 18.3 (2)	±1.6 (2)	±10.6 (2)	±7.3 (2)	±0.1 (2)	±2.8 (2)	±0.8 (2)	
	Female	250–300	267.6	24.0	67.1	78.6	22.3	22.8	81.3	
			± 11.5 (5)	±0.8 (5)	±1.8 (5)	±1.4 (5)	±1.6 (5)	±2.1 (5)	±1.8 (5)	
		200–250	218.2	25.7	68.2	83	24.2	26.0	79.7	
			± 7.8 (3)	±0.5 (3)	±2.8 (3)	±1.2 (3)	±3.6 (3)	±3.5 (3)	±0.6 (3)	
		250–300	270.5	25.9	67.6	80.7	22.3	23.1	83.7	
			(1)	(1)	(1)	(1)	(1)	(1)	(1)	
>300	387.3	22	67.8	78.6	21.1	19.9	80.7			
± 21.7 (4)	±0.0 (4)	±0.0 (4)	±0.0 (4)	±0.0 (4)	±0.0 (4)	±0.0 (4)	±0.0 (4)			
<i>E. sp. aff. dentata</i> [Johnstone]	Unsexed	0–200	92.3	28.8	69.9	81	26.2	34.4	80.6	
			± 4.4 (2)	(1)	±0.4 (2)	±3.5 (2)	±0.4 (2)	±1.0 (2)	±0.7 (2)	
	Male	200–250	215.6	24.5	62.5	74.7	22.8	22.8	79.1	
			± 5.1 (8)	±0.7 (8)	±2.6 (8)	±1.3 (8)	±2.5 (8)	±1.1 (8)	±2.4 (7)	
	Female	250–300	262.0	22.1	66.3	79.2	20.0	22.2	79.5	
			(1)	(1)	(1)	(1)	(1)	(1)	(1)	
	>300	250–300	267.4	24.3	66.3	76.5	22.5	19.9	83.0	
			(1)	(1)	(1)	(1)	(1)	(1)	(1)	
	324.9	24.3	67.5	72.1	23.5	20.4	39.1			
	± 30.7 (2)	±1.4 (2)	±4.6 (2)	±0.6 (2)	±4.0 (2)	±1.1 (2)	±55.4 (2)			
<i>E. lavarackorum</i>	Unsexed	0–200	154.8	24.0	66.1	82.5	22.7	22.7	78.1	
			± 27.8 (7)	±2.1 (7)	±1.4 (7)	±3.8 (7)	±2.4 (7)	±2.8 (7)	±3.0 (7)	
	Male	200–250	210.3	23.4	64.2	78.6	21.5	19.3	79.4	
			± 1.9 (3)	±0.6 (3)	±2.4 (3)	±1.1 (3)	±2.5 (3)	±1.3 (3)	±0.1 (2)	
	Female	200–250	210.5	24.2	65.8	77.2	24.4	18.8	80.0	
			± 13.0 (2)	±1.4 (2)	±0.3 (2)	±2.7 (2)	±0.0 (2)	±0.4 (2)	±1.2 (2)	
	>300	250–300	310.9	23.2	62.5	72.3	21.7	16.8	80.2	
			± 10.4 (2)	±0.1 (2)	±2.1 (2)	±1.5 (2)	±1.2 (2)	±0.5 (2)	±1.8 (2)	
	<i>E. irwini</i>	Unsexed	0–200	120	27.0	68.1	82.9	29.0	33.4	79.4
				± 23.2 (2)	±1.1 (2)	±5.6 (2)	±8.8 (2)	±0.4 (2)	±8.4 (2)	±2.0 (2)
Female		250–300	335.4	23.8	60.7	71.8	22.5	18.9	78.0	
± 15.7 (2)	±0.7 (2)	±2.5 (2)	±2.9 (2)	±2.2 (2)	±0.9 (2)	±4.4 (2)				
<i>E. dentata</i>	Unsexed	0–200	159.4	25.4	67.5	83.1	23.1	23	80.9	
			± 34.7 (9)	±2.0 (7)	±5.2 (9)	±3.4 (9)	±1.1 (9)	±2.8 (9)	±2.4 (8)	
	Male	200–250	239.3	24.7	61.7	75.7	20.6	17.2	82.0	
			± 12.5 (6)	±1.2 (6)	±1.9 (6)	±2.4 (6)	±1.7 (6)	±1.4 (6)	±1.9 (6)	
	Female	250–300	267.3	23.1	59.8	73.4	21.5	16.3	80.9	
			± 9.8 (8)	±1.4 (8)	±1.6 (8)	±1.1 (8)	±0.9 (8)	±1.1 (8)	±1.5 (7)	
	>300	200–250	200.0	25.1	64.8	80.2	21.7	17.1	81.8	
			(1)	(1)	(1)	(1)	(1)	(1)	(1)	
	250–300	>300	279.2	23.6	62.9	74.2	21.6	16.1	83.3	
			± 10.6 (10)	±2.1 (10)	±2.3 (10)	±3.4 (10)	±1.7 (10)	±0.7 (10)	±2.0 (9)	
314.3	19.7	63.1	74	20.7	15.2	81.8				
± 15.9 (2)	±5.7 (2)	±0.7 (2)	±4.6 (2)	±1.7 (2)	±2.2 (2)	(1)				

1. Abbreviations as per Appendix A. Means are given with standard deviations and sample sizes. Non-ratio measurements and ranges in mm.

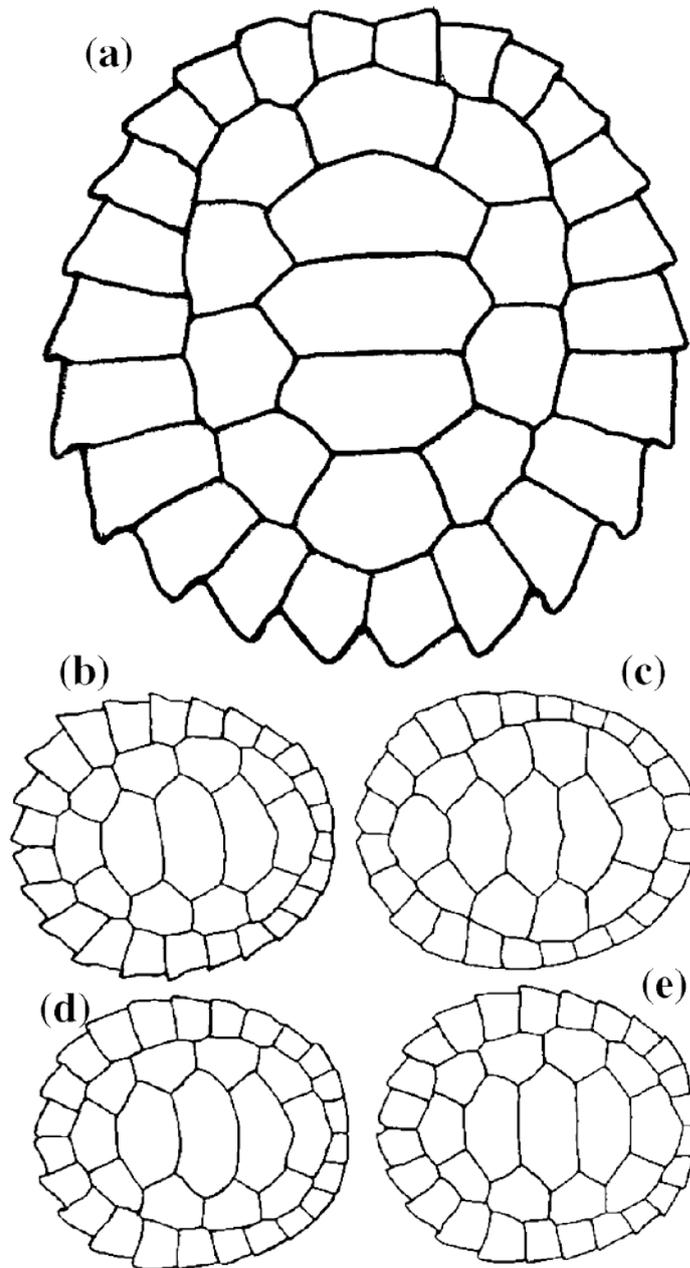


Figure 6. Dorsal view of the carapace for small juveniles of (a) *Elseya albagula* (Queensland Museum [QM] 36044, carapace length [CL] = 91.9 mm); (b) *Elseya lavarackorum* (unreg.); (c) *Elseya* sp. [Johnstone]; (d) *Elseya irwini* (paratype QM 59021, CL = 103.6 mm); and (e) *Elseya dentata* (Australian Museum [AM] 45481, CL = 120.5 mm). Refer also to Fig. 1.

cream, grey, and often suffused with pink in life; surrounded by small scales of low relief.

Boundary between pupil and iris indistinct (Fig. 7), occasionally with a vague lighter ring of gold flecks around the pupil. Iris dull brownish olive, not bright; sclera brown; leading and trailing eyespots absent. Upper eyelid with nine scales.

Dorsal surface of neck with medium rounded tubercles. Dark grey above, cream, yellow, or white below in females, typically light grey below in males but also may be cream, yellow, or white below as in females. As with head, boundary between light ventral coloration and darker dorsal coloration irregular and varies greatly among individuals.

Limbs and tail dark grey above, light grey below with or without irregular blotches (see allotype, Fig. 2). In some adult females, and rarely in males, the distinctive light coloration of the ventral and lateral surfaces of the head and neck may extend down the forelimbs. Five claws on the front feet; four on the rear. A series of enlarged scales present on the leading and trailing edges of the lower limb; may be present on the thigh. Pre-anal glands absent.

Dorsal color of the head and soft parts of juveniles follows that of the carapace. Ventral base color cream suffused vaguely with yellow or orange. Ventral surfaces of tail and hindlimbs noticeably brighter, forelimbs duller; no distinct striping on limbs or tail. Most neck tubercles are pale olive. A vague stripe extends from the angle of the mouth two-thirds of the way to the shoulder, including the lower tympanum. Ventral surface of head and neck cream or yellow, with a slight gold or orange suffusion on chin and gular region.

Size and Sexual Dimorphism. — This species is among Australia's largest side-necked turtles, with possibly only *Elusor macrurus* attaining a larger size (J. Cann, pers. comm., 1997). Females grow to a larger size than males (females to 420 mm CL, Mary River [M. Dorse, pers. comm., 2004]; males to ca. 300 mm). Largest examples in this study were a 418-mm female and a 275mm male. Males easily distinguished from mature females by a much larger tail (Figs. 1 and 2), as with all shortnecked chelids, however, sex of animals up to 150-mm CL could not be determined with confidence.

Osteology

Skull. — Skull large and robust, emarginated both from below and behind (Fig. 4, n = 5), but to a much lesser degree than *E. dentata* (*sensu stricto*) (n = 12). Temporal emargination greater than in any other Queensland *Elseya*; parietal arch wider but not to the extent that it can support the attachment of a head shield. Alveolar ridge extensive, but not to the extent

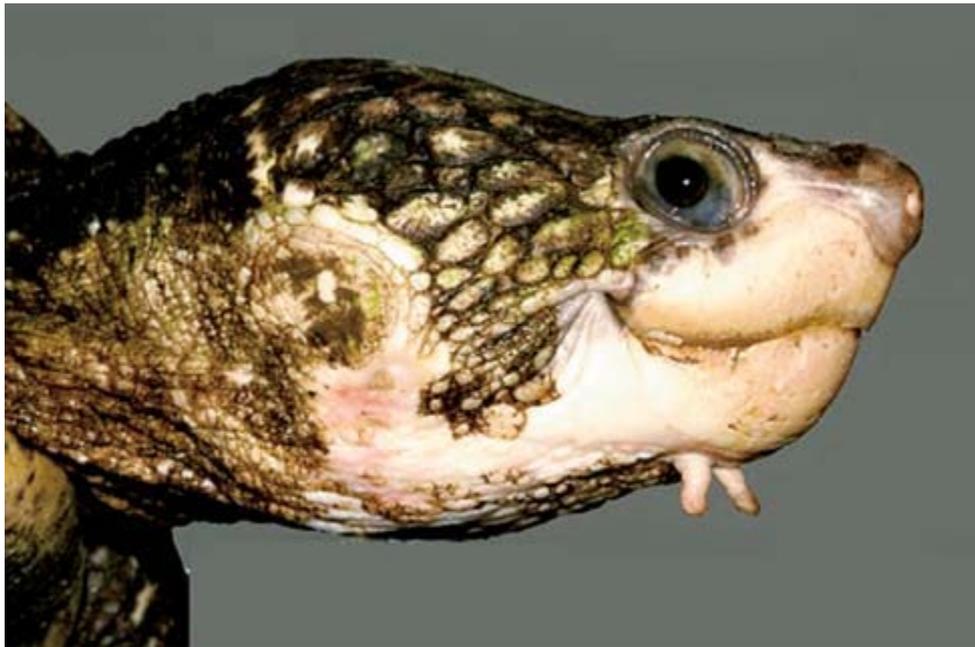


Figure 7. Lateral view of the head of the female holotype of *Eseya albagula* (Queensland Museum J81785, carapace length = 382.4 mm). Note the prominent barbels, prominent tomial sheath, prominent scales on the temporal region, and pupil indistinct from iris.

of *E. lavarackorum* (Fig. 8, n = 2), beginning adjacent to the premaxilla lateral to the *foramen praepalatinum*. Alveolar ridge extends back to the end of the triturating surface; does not contact the palatines. Lingual ridge of the triturating surface heavily serrated and widened throughout its length; almost obscures the *apertura nasalis interna* and completely obscures the *foramen praepalatinum* from ventral view. The ridge extends back to almost make contact with the pterygoids but does not obscure the anterior edge of the vomer, differentiating it from *E. lavarackorum*. The lingual ridge is on the premaxilla in the anterior skull and continues onto the maxilla but adjacent to the medial edge of the *apertura nasalis interna* it continues onto the palatine bone. The degree of serrating is moderate but second only to *E. lavarackorum* in its widening of the triturating surface. The maxilla and palatines are significantly thickened and the *apertura nasalis internae* are deeply recessed into the palatal surface of the skull.

Vomer and the pterygoids not in contact; vomer not expanded posteriorly but separates the anterior two thirds of the palatines, a character that distinguishes this species from *E. lavarackorum* and *E. sp. aff. dentata* (Johnstone) (n = 4)—the vomer is expanded posteriorly in *E. lavarackorum* and only divides the anterior half of the palatines in *E. sp. aff. dentata* (Johnstone). *Canalis caroticus internus* closed. Foramen *anterioris canalis carociti interni* absent.

Ventral surface of the skull below the foramen *nervi trigemini* constricted to the same width as the braincase. In other *Elseya* this section is significantly wider than the braincase. Supraoccipital is extremely small dorsally, does not divide the parietals but lies posteriorly to them at the rear of the skull. *Crista supraoccipitalis* short, extending beyond the occipital condyle, but not to the same extent as in *E. dentata*.

Cervicals. — Articulation formula (Williams 1950) is the same as for all chelid turtles: (2(, (3(, (4(, (5),)6),)7(, (8). The atlas-axis complex (Hoffstetter and Gasc 1969) is made up of two neural arches and the first centrum ventrally and an intercentrum anteriorly, these units are fused as in the primitive condition for many turtle species. Centra of remaining cervicals have well-developed sagittal blades that are more prominent at the anterior end of the series and also at the anterior half of each centrum. Each sagittal blade straight in lateral view and narrow, except for the eighth cervical, which is markedly thickened. Transverse processes large, triangular, occupying the middle-third of the centrum and protruding horizontally from the neural arch; not angling downwards as in many other species. Postzygapophoses extremely large and almost joining in the midline; robust in overall structure.

Prezygapophoses smaller and extending upwards to meet the postzygapophoses of the preceding vertebrae. Neural spine present but small.

Shell. — Anterior bridge buttress poorly developed (n = 6). Anterior bridge strut suture with a widely spaced anterior and posterior component, a feature shared with *E. lavarackorum* (n = 4), *E. sp. aff. dentata* (Johnstone) (n = 4), and *E. irwini* (n = 1); no prominent medial constriction. Posterior bridge strut well developed, in significant contact with the fifth pleural. Exposed neurals absent.

Multivariate Comparisons

Species in the *E. dentata* generic group are conservative in body form, and this is reflected in the outcome of discriminant function analyses. For females, four ratio variables contributed significantly to discrimination among species (Fig. 8a): V2/V1 ($R^2 = 0.70$, $F = 13.52$, $p = 0.0001$), IO/HL (partial $R^2 = 0.44$, $F = 4.34$, $p = 0.01$), HW/CL (partial $R^2 = 0.47$, $F = 4.38$, $p = 0.02$), and IO/OD (partial $R^2 = 0.40$, $F = 3.57$, $p = 0.05$). Refer to Appendix A for details of measurements. Canonical variant 1 explained 47.8% and canonical variant 2 explained 45.7% of the variation among group centroids. For males, three ratio variables contributed significantly to discrimination among species (Fig. 8b): V2/CL ($R^2 = 0.82$, $F = 44.96$, $p = 0.0001$), OD/HL (partial $R^2 = 0.40$, $F = 5.99$, $p = 0.005$), and HW/CL (partial $R^2 = 0.30$, $F = 3.78$, $p = 0.05$). Canonical variate 1 explained 80.5%, and canonical variate 2 explained 19.4% of the variation among group centroids. Crossvalidation error rates in classification to species were 22.1% for females and 4.1% for males (Table 4). Hence, on the basis of the measurements included in this analysis, discrimination between *E. albagula* and the other species is not diagnostic (Table 4), reflecting the conservatism in overall body form among species in this group.

Ecology

Habitat. — This species is widely distributed within the river systems it occupies, from the permanent waters of the uppermost spring-fed pools to the freshwater-brackish water interface (Hamann et al. 2004). It prefers flowing waters with complex subsurface structure in the form of log tangles, undercut banks, and irregular rocky substrata. It is typically absent or rare in standing waters impounded by dams or weirs, unless associated with free-flowing streams. It does not inhabit brackish waters.

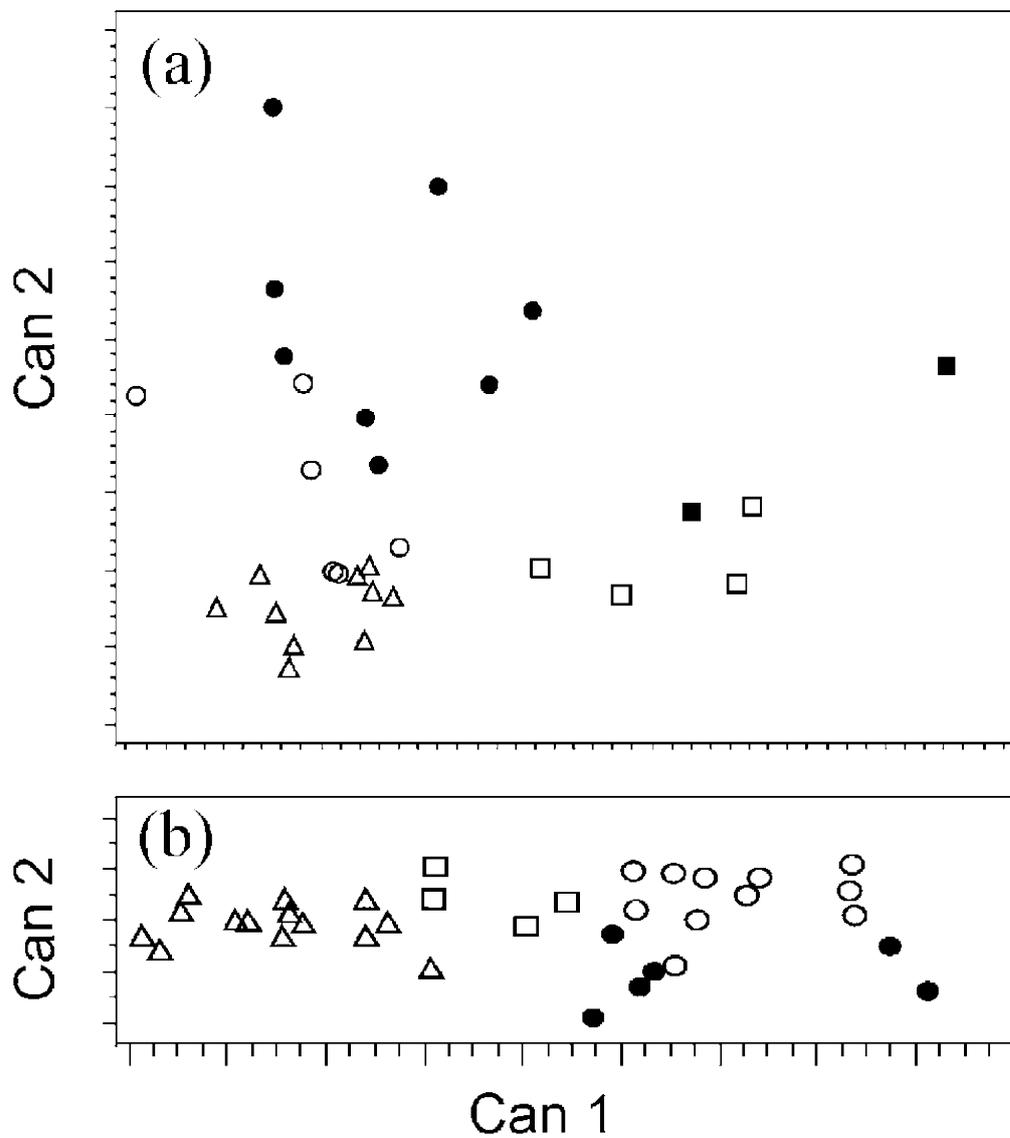


Figure 8. Specimens of *Elseya albagula* (●), *Elseya* sp. [Johnstone] (○), *Elseya dentata* (△), *Elseya lavarackorum* (□) and *Elseya irwini* (■) plotted in canonical variate space: (a) females; (b) males. Axis lengths in proportion to the percentage of variation among species centroids explained by the canonical variates.

Table 4. Results of cross-validation for the discriminant analysis of males and females. Discrimination between *E. albagula* and the other species is not diagnostic, reflecting the conservatism in overall body form among species in this group. Data shown are Males/ Females.

	<i>E. dentata</i>	<i>E. irwini</i>	<i>E. lavarackorum</i>	<i>E. sp. aff. dentata</i> [Johnstone]	<i>E. albagula</i>
<i>E. dentata</i>	13/11	-/0	1/2	0/0	0/0
<i>E. irwini</i>	-/0	-/1	-/1	-/0	-/0
<i>E. lavarackorum</i>	0/0	-/0	4/4	0/0	0/0
<i>E. sp. aff. dentata</i> [Johnstone]	0/0	-/0	0/0	10/4	1/1
<i>E. albagula</i>	0/1	-/0	0/0	0/1	6/6

Reproductive Cycles. — The peak breeding season for males is between January and August. Females leave the water once per year between March and September to lay approximately 14 hard-shelled eggs (Hamann et al. 2004). The nest is constructed mostly on the front face and top of steep sloping banks with sand or soil substrates. Nest and hatchling predation by pigs, dogs, foxes, cats, monitor lizards, and water rats is intense. Many of these predators are exotic and their activity, coupled with habitat modification, is regarded as a major threat the persistence of the species in many parts of its range (Hamann et al. 2004).

Diet. — *Eelseya albagula* is primarily herbivorous, feeding on fruit and buds of riparian vegetation that falls upon the water, filamentous algae, and instream macrophytes. Animal material forms a small part of the diet of adults and includes freshwater sponges and carrion. Young may be more carnivorous. In captivity, the young feed readily on snails.

Discussion

Eelseya albagula is distinctive not least by virtue of its large size and resides in an area of high human population. It is remarkable that it is only now being described, but it cannot be regarded as a new discovery. *Eelseya dentata* (Gray 1863) has long been suspected to be a species complex. Both Goode (1967) and Cann (1978) recognized the distinction between populations from the Northern Territory and east coastal Queensland, and anticipated reclassification of the distinctive forms. Legler (1981) recognized five distinguishable allopatric populations of what was then regarded as *E. dentata*: (1) populations in the Ord, Victoria, and Daly systems, and possibly eastward to the Alligator rivers region; (2) populations in the Roper and Nicholson-Leichhardt drainages of the Gulf of Carpentaria; (3) the north Johnstone River system of east coastal Queensland; and (4) all populations south of the Atherton tableland, including the Fitzroy River and Burnett River populations. Allozyme studies, using sampling designs based on the extensive field work by Cann, confirmed the existence of a number of genetically distinctive forms, that were sufficiently divergent to be regarded as separate biological species (Georges and Adams 1992, 1996) including with some variation, those identified by the above authors. These new forms are being described progressively (Cann 1997b; Thomson et al. 1997), with this paper contributing to that progress.

We regard the species as comprising populations from the Mary, Burnett, and Fitzroy-Dawson drainage basins. Recent work using a combination of nuclear and mitochondrial markers reveal some genetic differentiation between these three drainages and within the

larger Fitzroy-Dawson drainage, but there are no fixed differences established using the nuclear markers (Farley et al., forthcoming). We interpret this substructuring as the accumulation of genetic differences among populations of a single species since their isolation by distance and recent sea level rise. Thus, in our view, the populations in the three river drainages represent three contemporary evolutionary significant units (Moritz 1994) within a single morphologically well-defined biological species.

Conservation Considerations. — *Elseya albagula* is widespread and locally abundant in three major drainage basins of southeastern Queensland (Hamann et al. 2004), and as such may currently be regarded as secure. The predominance of adults in all populations is a concern (Hamann et al. 2004) and possibly exacerbated by heavy predation by exotic predators. In addition, the species is intrinsically vulnerable by virtue of its specialized habitat requirements, namely a reliance on flowing waters and riffle, reinforced by its dual mode of respiration (Legler and Georges 1993; FitzGibbon 1998). Flowing waters are coming under increasing threat from water resource development, and particularly the development of new impoundments or redevelopment of existing impoundments to service the needs of agriculture, industry, and urban centres. *Elseya albagula* would be a good candidate for monitoring as a sensitive indicator of riverine health.

Appendix A: Descriptions of Measurement Used

Skull Measurements. — HL (Head Length), straight line from base of nose to the back of the crista supraoccipitalis; HW (Head Width at Tympanum), maximum straight width of skull at tympanum; PW (Parietal Width), width of skull at juncture of the parietals and frontal; IO (Interocular Width), width of frontal bone between the orbits; OD (Ocular Diameter), horizontal maximum straight-line diameter of the orbit.

Shell Measurements. — CL (Carapace Length) from the cervical, or junction of the first marginals, to the suprapygal; CW4 (Carapace Width 4), straight width at the junction of the fourth and fifth marginal scutes; CW8 (Carapace Width 8), straight width of carapace at the juncture of the seventh and eighth marginal scutes; V1 (Width Vertebral 1), maximum width of the first vertebral scute; V2 (Width Vertebral 2), maximum width of the second vertebral scute; PL (Plastron Length), maximum midline length of the plastron.

Ratio Variables. — 1. HL/CL; 2. IO/HL; 3. OD/HL; 4. PW/HL; 5. CW4/CL; 6. CW8/CL; 7. V1/CL; 8. V2/CL; 9. PL/CL; 10. CW4/CW8; 11. V2/V1; 12. IO/OD; 13. PW/HW; 14. PW/HL.

Appendix B: Specimens Examined

Abbreviations used: AM, Australian Museum; AMNH, American Museum of Natural History, New York; ANWC, National Wildlife Collection; NHM, Natural History Museum of London; MV, Museum of Victoria; NTM, Museums and Art Galleries of the Northern Territory; QM, Queensland Museum; RMNH, Nationaal Natuurhistorisch Museum, Leiden; UU, University of Utah collection of J.M. Legler; WAM, Western Australian Museum; UC, University of Canberra collection of the senior author; NT, Northern Territory; WA, Western Australia; QLD, Queensland; NSW, New South Wales.

Elseya albagula: Fitzroy-Dawson Drainage. — UU 17898–903 Connors River 3.5 km W, 3.0 km S, Connors River (22°13'S, 149°01'E); QM 48615 Belmont Creek, Fitzroy River (23°16'S, 150°28'E); QM 37933 Dawson River Crossing, at Baroondah Station (25°41'S, 149°13'E); QM 47987, 47998, 48002, 48010, 48039 Dawson River, Theodore (24°57'S, 150°05'E); QM 28449 Emerald, Nogo River, Town Weir (23°31'S, 148°01'E); UU 17096–102 Fitzroy River 63 km N, 25 km E Duaringa (23°11'S, 149°55'E); QM 38533 Rockhampton, lagoon 18 km W (23°17'S, 150°25'E); UU 17093–5, 17274 Raglan Creek 12.5 km W and 1.5 km N Mt. Larcom (23°49'S, 150°52'E); UU 17874–81, 17888–97 Raglan Creek 3.7 km E, 8.5 km S Raglan (23°48'S, 150°51'E); AM 129338–40, QM 59269 Raglan Creek, nr. Raglan (23°38'S, 150°49'E); UU 17882–7 Raglan Creek, 5.5 km W, 9.3 km S Raglan (23°48'S, 150°46'E). Burnett River – QM J81785, 59270 Walla Weir, Burnett River (25°03'S, 152°05'E); UU 17086–92 Barambah Creek 7.8 km S, 9.2 km E Gayndah (25°41'S, 150°48'E); UU 14872 Barambah Creek 3.2 mi E, 2.8 mi N Gayndah (25°35'S, 151°40'E); QM 48026 Burnett River, Grays Waterhole, nr. Gayndah (25°37'S, 151°37'E); QM 48029, 48052 Burnett River, Jones Weir (25°36'S, 151°18'E); QM 48027 Burnett River, Munduberra (25°35'S, 151°18'E); QM 48012, 48046 Burnett River, nr. Gayndah (25°37'S, 151°37'E); QM 2966, AM 6110, Eidsvold (25°22'S, 151°07'E); NHM 75.5.4.8, 76.5.19.77, 1875.5.4.7–8, QM 4501, 4505 Gayndah (25°37'S, 151°37'E); AM 123067 Grey's Waterhole, Burnett River (25°32'S, 151°39'E). Mary River – UC 0305–6 Mary River; QM 36036, 36042, 36045 Tuan State Forest, Tinana Creek, Missings Bridge (25°41'S, 152°53'E); QM 36039, 36041, 36044, 36046–7, 59271 Coondoo Creek, Tin Can Bay Road (25°59'S, 152°50'E).

Elseya dentata: King Edward River. — WA 28119, UU 18518 Kalumbaru (14°18'S, 126°38'E). Ord River – WA 47723, NTM 7057 Dunham River (16°16'S, 128°11'E); UU 14793–800 East Baines R. 7 mi S, 3 mi E, Auvergne (Bula) (15°47'S, 130°03'E). Victoria River – MV 10406, AM 72947–57, 75070–1, 88442, 93490, NTM 13523, MV 10384–90, 10402–5, 10827–35 Jasper Gorge (16°2'S, 130°41'E); UU 14777 Timber Creek., Timber Creek Store (15°42'S, 130°29'E); MV 10397–9, 10781, 10846, 10850, 10858–60 Timber Creek (15°39'S, 130°29'E); NHM 1947.3.6.2–3, 1947.3.4.14 upper Victoria River; NTM 13521 Victoria River (15°38'S, 131°08'E); NTM 32972 Victoria River (17°35'S, 130°05'E); WA 36998–37000 Bullo River (15°40'S, 129°40'E); AM 72692–4, 72934–46, 73346, 79160 Bullo River at crossing of Katherine – Kununurra Road (15°42'S, 129°38'E); MV 10871–4 Tortoise Reach, Fitzroy Station (15°33'S, 130°52'E). Daly River – NTM 32970 18 km NE of Katherine (14°23'S, 132°24'E); NTM 43, 4633 Claravale Crossing, Daly River (14°22'S, 131°33'E); UU 14840–4 Daly R. 2 mi W Claravale Homestead (14°20'S, 131°33'E); UU 14809 Daly R. (prob. Edith R. 14 mi NW Katherine) (14°20'S, 131°33'E); AM 31725 Daly River (14°28'S, 131°41'E); NTM 1220–3, 21152–4 Daly River (13°55'S, 130°56'E); NTM 17201, 17205–6, 17210, UC 0309–19, 0328 Douglas River (13°47'S, 131°17'E); UU 14810–36 Edith Falls, 19.5 mi N, 5 mi W of Katherine (14°12'S, 132°14'E); AM 31728, NTM 13317–21 Edith River (14°28'S, 132°02'E); WA 16516–7, 19906–8, 21594, 24939–40 Katherine (14°30'S, 132°13'E); NTM 3710–3, 3825, 5170, 6583, 32971, AM 45481, 43533 Katherine River (14°28'S, 132°16'E); NTM 13436, 13510 Ooloo Crossing, Daly River (14°04'S, 131°15'E); UU 14837–8 Seventeen Mile Creek 11 mi N 11 mi E Katherine (14°18'S, 132°25'E); UU 14839 Ferguson River, 23 mi N, 18 mi W of Katherine (14°04'S, 131°58'E); NTM 2973 Daly River (14°41'S, 131°34'E). Darwin Region – NTM 7058 Casuarina (12°23'S, 130°54'E); NTM 34498 Darwin (12°27'S, 130°50'E); NTM 34497 Howard Springs (12°27'S, 131°03'E); NTM 21922 Sandy Creek, Litchfield National Park (13°16'S, 130°44'E); UU 14776 Finnis R. (35 mi S Darwin) (13°04'S, 130°58'E); NTM 21717 Tjaynara Falls, Litchfield National Park (13°15'S, 130°44'E); UU 14774–5 Adelaide Drainage, 60 mi S, 12 mi E Darwin (12°34'S, 131°24'E). Alligator Rivers Region – UU 14784–92 Barramundie Creek 3 mi S, 7 mi W Spring Peak (13°01'S, 132°23'E).

Elseya lavarackorum: Roper River. — NTM 16328–30 Red Lilly Lagoon, Roper River (14°42'S, 134°05'E); UU 14779–82 Roper River 1.5 mi W Elsey Homestead (14°59'S, 133°19'E); UU 14778 Roper River Elsey Homestead (14°58'S, 133°20'E). Gregory-Nicholson Drainage – QM 47908, 47911, 48547, 48564 Elizabeth Gorge, Bowthorn Station (18°13'S, 138°20'E); UU 14801–8 Gregory River 3.7 mi S, 3.7 mi W Gregory Downs

(17°53'S, 139°17'E); QM 31939, 31942, 31944, 31946–7, 31949–50, 31952 Gregory River, Riversleigh Station, N of Mt Isa (19°02'S, 138°45'E); UC 0201, QM 48544 Lawn Hill Gorge (18°46'S, 138°25'E); QM 46284 Lawn Hill National Park (18°35'S, 138°35'E). Roper River – UU 14783 Waterhouse River, 1 mi S, 1 mi E Mataranka Homestead (14°55'S, 133°08'E); AM 13219 Mataranka (14°56'S, 133°04'E).

Elseya irwini: Burdekin River. — ANWC 0520 Townsville (19°16'S, 146°49'E); QM 59431 Burdekin River (19°42'S, 147°18'E); QM 59021 Junction of Bowen River and Sandlewood Creek, Burdekin Drainage (20°27'S, 147°24'E).

Elseya sp. aff. dentata (South Alligator) (Voucher Label, Georges and Adams, 1992): Mary River. — UC 0304 Corroboree Billabong, Mary River. Alligator Rivers Region – UU 18746–7 Barramundie Creek, 9 km S, 7 km W of Spring Peak (14°49'S, 126°30'E); UU 18740–5 Barramundie Creek, 9 km S, 7 km W, Spring Peak (13°03'S, 132°23'E); UU 18748 Barramundie Gorge, 88 km SW Jabiru (13°19'S, 132°26'E); UU 17908–40, 18755–6, AM 129342 Bowerbird Lagoon, 15 km S, 16 km E of Jabiru (12°47'S, 133°03'E); NTM 34496, NWC 0531, AM 43532 Deaf Adder Creek (13°04'S, 132°58'E); UU 17906–7 Double Billabong, E. Alligator River, Arnhem Land (13°09'S, 133°22'E); UU 18757–9 East Alligator River, Arnhem Land (13°12'S, 133°19'E); UU 18749 Graveside Pool, Jim Jim Drainage (13°16'S, 132°35'E); UU 17949–53, 18750–1; AM 128001–4 Magela Creek (12°29'S, 132°52'E); NTM 13985 Pul Pul Billabong, South Alligator River (13°34'S, 132°35'E); UU 17904–5 Right Angle Pool, E. Alligator River (12°53'S, 133°25'E); UU 17941–8 Sandy Billabong 11 km S, 11 km E Nourlangie Camp (12°52'S, 132°46'E); UU 18752–4 South Alligator R. 10 km SE El Sharana (13°34'S, 132°35'E); NTM 13512 South Alligator River (13°30'S, 132°28'E); AM 38325–6 Koongarra, Brockman Range, Arnhem Land (12°47'S, 132°39'E). Mann River – AM 40278 Mann River, Liverpool River drainage (31°28'S, 146°39'E). Goyder River – AM 40181 Goyder River (12°56'S, 135°01'E).

Elseya sp. aff. dentata (Johnstone) (Voucher Label, Georges and Adams, 1992): Cairns District. — AM 68848, 93048 Cairns district (168550S, 1458460E); QM 48062, 48068 Hartley Creek (158460S, 1458190E); AM 125468, QM 23053–4, 23056–7, 23060, 23175–6, 23299–300, 23322, 28954, UU 14845–71 Malanda, North Johnstone River (178210S, 1458350E); QM 48060 nr. Cairns (168550S, 1458460E); QM 48059, 48064–5 South Johnstone River (178380S, 1458050E).

Chapter 7: *Myuchelys* gen. nov. — a new genus for *Elseya latisternum* and related forms of Australian freshwater turtle (Testudines: Pleurodira: Chelidae).

Published as: Thomson, S. and Georges, A. 2009. *Myuchelys* gen. nov.—a new genus for *Elseya latisternum* and related forms of Australian freshwater turtle (Testudines: Pleurodira: Chelidae). *Zootaxa* 2053:32–42.

Abstract

Myuchelys, a new genus, is erected for a well-supported clade of Australasian freshwater turtles; its establishment resolves an unacceptable paraphyly in relationships among species of the genus *Elseya*. Molecular and morphological evidence indicates that the closest relationship of the new genus is with *Emydura*, not the redefined *Elseya*.

Keywords: Phylogeny; paraphyly; side-necked turtle; sawshelled turtle

Introduction

The genus *Elseya* has had a long and confused history. It was erected by Gray (1867) for the species *Chelymys* [now *Elseya*] *dentata* Gray, 1863 and *Elseya latisternum* Gray 1867. *Elseya dentata* was later designated as the type species (Lindholm, 1929). The genus was diagnosed by the presence of a horny shield on the dorsal surface of the head; flat polygonal plates on the temples, cheeks and throat; prominent tubercles on the dorsal surface of the neck; a pair of tubercles on the chin; and the usual absence of a cervical scute (Gray, 1867; Gray, 1872). Boulenger (1889) redefined the genus, placing significance on the alveolar ridge (a longitudinal ridge on the triturating surface of the maxillary sheath and underlying bone) as a character, then known to be present only in *Elseya dentata*. *Elseya latisternum* and *Elseya novaeguineae* (Meyer, 1874) lack the alveolar ridge, and so Boulenger placed them in the genus *Emydura*. Later, Goode (1967) disagreed with the importance placed on the alveolar ridge, noting that well-established cryptodiran genera displayed considerable variation in this character, and returned *E. latisternum* and *E. novaeguineae* to the genus *Elseya*.

Elseya novaeguineae, *Emydura signata* Ahl, 1932 and *Emydura subglobosa* (Krefft, 1876), as defined in 1980, were virtually indistinguishable using total serum protein

electrophoresis and were very closely related to *Elseya latisternum* (Frair, 1980). Their karyotypes are identical, with a diploid number of 50 (Bull & Legler, 1980), and Gaffney (1977) could not consistently differentiate the various taxa using skull morphology. McDowell (1983) considered a wide range of morphological characters and concluded that the closest relatives of *Elseya dentata* are among the species of *Emydura*, not *Elseya latisternum*. Frair (1980), Gaffney (1977), and McDowell (1983) all argued for synonymising *Emydura* and *Elseya*, but that recommendation has not gained wide acceptance. The paraphyletic arrangement of species within *Elseya* was well established with the addition of molecular evidence (Georges & Adams, 1992; Seddon, et al., 1997; Georges, et al., 1998) and the descriptions of *Elusor* (Cann and Legler 1994) and *Rheodytes* (Legler and Cann 1980) (see Megirian & Murray, 1999).

The purpose of this paper is to resolve the unacceptable paraphyletic relationship among the species of *Elseya* by splitting them into two monophyletic genera.

***Myuchelys*, gen. nov.**

Type species. *Elseya latisternum* Gray, 1867 designated herein.

Etymology. The name is a combination of a contraction of the Aboriginal word for clear water, *Myuna*, and the Greek word for tortoises, *chelys*. It is a generalized reference to the types of habitat often preferred by the species of this genus.

Diagnosis. A member of the short-necked chelid turtles of the Australasian region which, excluding *Pseudemydura umbrina* (Siebenrock, 1901), together form a well-established clade (Georges & Adams, 1992; Georges, et al., 1998). Differs from other short-necked turtles of the clade in possessing the following combination of characters (Table 1): Absence of a well-developed alveolar ridge on the triturating surfaces and underlying bones of the jaw (Fig. 1B) (present only in the redefined *Elseya*, Fig. 1A); parietal arch of skull wide, nearly as wide as tympanum (Fig. 2) (narrower than the tympanum in *Elseya* and *Emydura*); large distinctive head shield, entire, that extends in part down the parietal arch toward the tympanum (absent in *Emydura*, not extending down the parietal arch in *Elseya*, *Rheodytes* and *Elusor*); ilium-carapace suture involves pleurals 7–8 and the pygal (as in *Elusor* but distinct from the condition in *Elseya* and *Emydura*); anterior bridge strut is confluent with the rib-gomphosis of pleural one; no angle of intersection between these two bony units when viewed ventrally (as in *Elusor*, but unlike *Elseya*, *Emydura* and *Rheodytes* – see Fig. 1 and 2 of Thomson, et al., 1997).

Table 1. Distribution of character states among taxa utilized in the cladistics analysis. Characters are described in the Appendix.

Character	<i>Myuchelys</i>	<i>Pseudemydura</i>	<i>Rheodytes</i>	<i>Elusor</i>	<i>Elseya</i>	<i>Emydura</i>	<i>Chelodina</i>	<i>Phrynops</i>
1	0	0	0	0	1	0	0	0
2	0	0	1	1	1	2	2	0
3	0	0	0	0	1	0	0	0
4	0	0	0	0	1	1	2	0
5	0	1	0	0	0	0	0	0
6	0	0	0	0	2	1	0	0
7	1	1	1	1	1	1	0	0
8	0	0	0	0	1	1	0	0
9	0	0	0	0	0	0	1	0
10	0	1	0	0	0	0	0	0
11	0	0	0	0	0	0	1	0
12	0	0	0	0	0	0	1	0
13	0	0	0	0	0	0	1	0
14	0	1	0	0	0	0	0	0
15	1	2	1	1	1	1	3	0
16	0	1	0	0	0	0	0	0
17	0	1	0	0	0	0	0	0
18	0	1	0	0	0	0	0	0
19	0	0	0	0	0	0	1	0
20	1	1	1	1	1	1	0	0
21	0	0	0	0	0	0	1	0
22	1	0	1	1	1	1	0	0
23	0	1	0	0	0	0	0	0
24	0	0	0	0	0	0	1	1
25	0	0	1	0	1	1	0	0
26	1	1	0	1	2	3	0	0
27	0	0	0	0	1	1	0	0
28	0	0	0	0	1	0	1	1
29	0	1	0	0	1	0	0	0
30	0	0	1	0	2	1	0	0
31	0	0	2	1	1	1	0	0
32	0	1	1	1	1	1	0	0
33	0	1	0	0	0	0	1	1
34	0	0	0	0	0	0	1	0
35	0	0	1	1	1	1	0	0
36	0	0	0	0	1	1	0	0
37	0	0	0	0	0	0	1	0
38	0	0	0	0	0	0	1	0
39	0	0	0	0	0	0	1	0
40	1	0	1	1	1	1	0	0
41	0	0	0	0	0	0	1	0
42	0	0	0	1	1	1	0	0
43	1	?	0	0	0	0	0	?
44	0	?	1	0	0	1	0	?

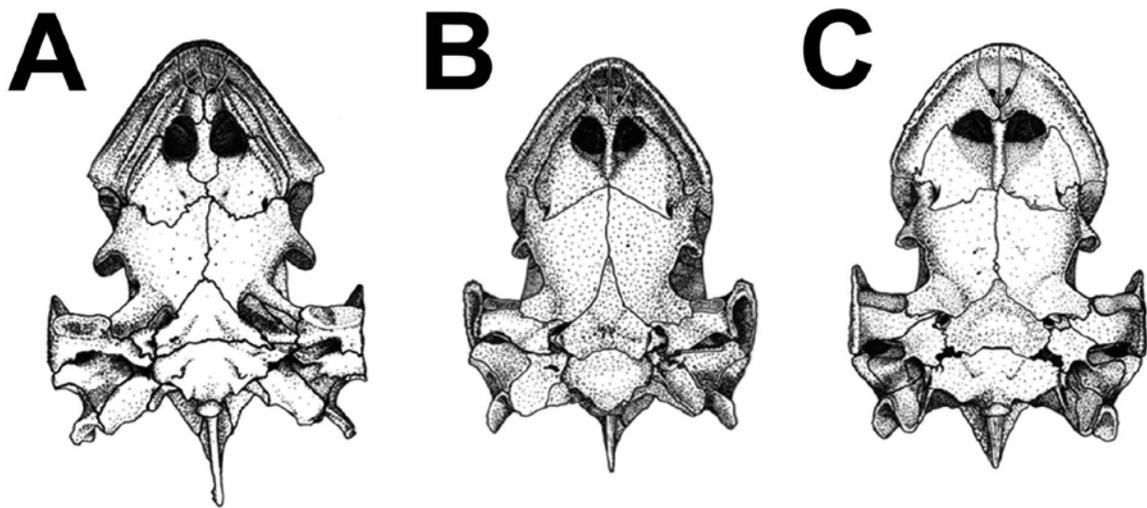


Figure 1. Ventral view of the skulls of **A.** *Elseya dentata* (UC0302); **B.** *Myuchelys latisternum* (AM 125475) and **C.** *Emydura macquarii* (QM48034). Note the alveolar ridge on the maxillary surface of *Elseya dentata*.

Description. Medium-sized turtles with a broadly oval carapace that is dorso-ventrally flattened and dark brown to black in colour, depending on species. Cervical scute typically present, though present only as a rare variant in most populations of *M. latisternum* north of the NSW–Queensland border (Legler & Cann, 1980). Plastron narrow, anterior lobe distinctly wider than posterior lobe. Plastron grey, light cream or yellow often with dark streaking or blotching, especially at the leading growth edge of plastral scutes and ventral surfaces of the marginal scutes. Intergular scute highly variable, but typically as wide as the adjacent gulars. Bridge carapace suture is narrowest medially and at its widest on the peripheral edge of the bridge strut region. Rib-gomphosis of pleural five inserts into the center of peripheral seven; ilium-carapace suture involves pleurals seven, eight and the pygal bone. Parietal arch of skull is wide, nearly as wide as tympanum; crista supraoccipitalis short does not extend past crista paroccipitalis. Lingual ridge small, unmodified.

Species. *Myuchelys latisternum* (Gray, 1867), *M. georgesi* (Cann, 1997a; *Elseya* [var. Bellingier] in Georges & Adams, 1992;1996), *M. purvisi* (Wells & Wellington, 1985; *Elseya* [var. Manning] in Georges & Adams, 1992;1996) and *M. bellii* (Gray, 1844; *Elseya* [var. Gwydir] in Georges & Adams, 1992;1996, resurrected by Cann, 1998) are assigned to the new genus. Molecular analyses by Georges and Adams (1992; 1996) verified the validity of each of these as biological species and showed that they formed a distinct clade. *Myuchelys purvisi* and *M. georgesi* are cryptic species (Georges & Adams, 1996; Thomson & Georges, 1996) differing overtly only in intensity of coloration.

Distribution. Species of *Myuchelys* are found in the coastal rivers of northern New South Wales north to Cape York and west to the Arnhem Land plateau of the Northern Territory (Georges & Thomson, 2009). *Myuchelys bellii* is restricted to the tributaries of the Murray-Darling drainage basin that flow west from the Great Dividing Range in northern New South Wales. *Myuchelys georgesi* and *M. purvisi* are restricted to the Bellingier and Manning Rivers of coastal New South Wales, respectively. *Myuchelys latisternum* is the most widespread, ranging from the Richmond River (NSW) in the south to the Jardine River of Cape York in the north (Qld). Its distribution includes also the rivers that flow into the Gulf of Carpentaria and the headwater tributaries that drain the Arnhem Land plateau into the Roper, South Alligator and Daly Rivers of the Northern Territory. An isolated population is known from the headwaters of the Mary River in the Northern Territory in Kakadu National Park.

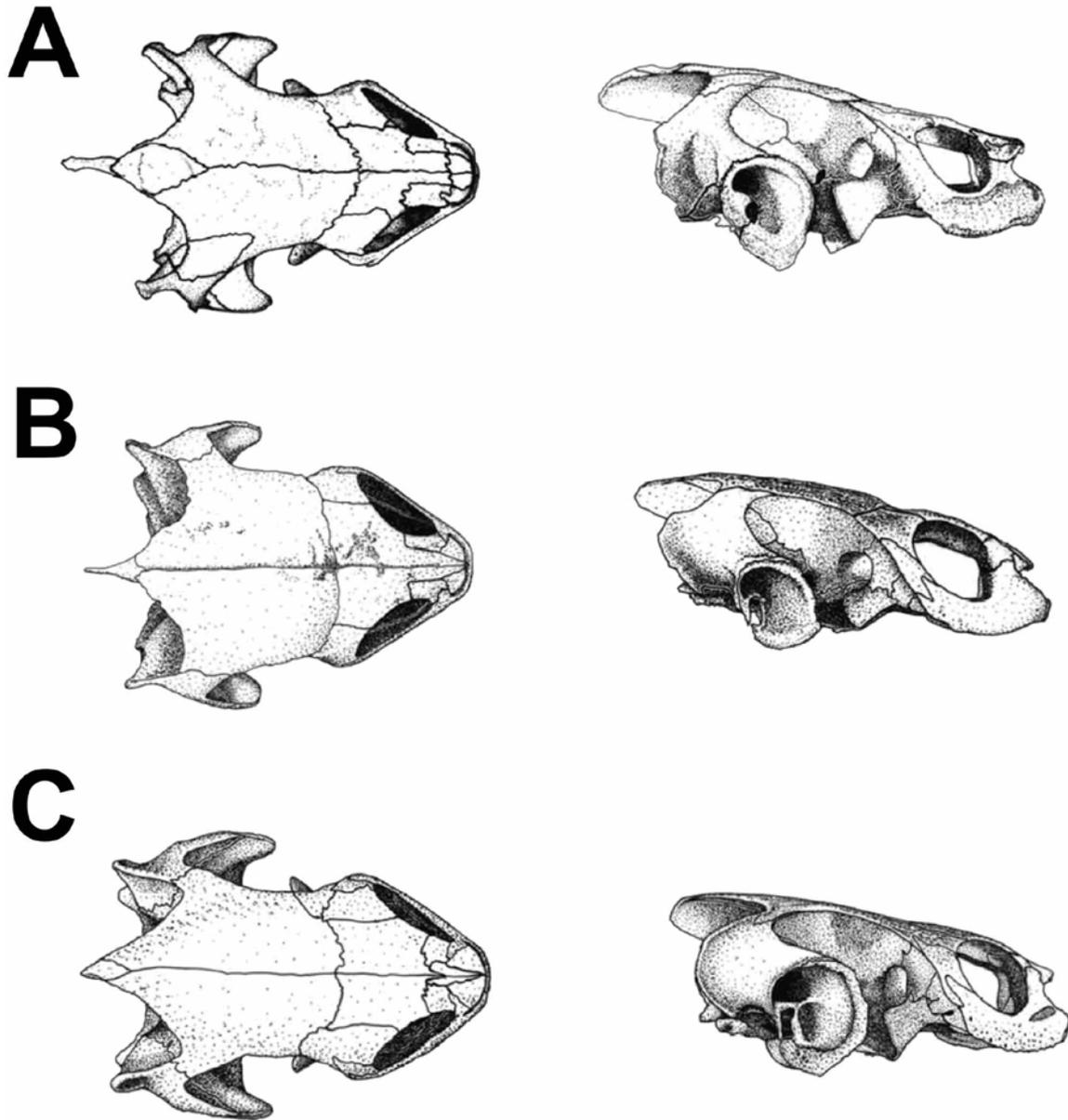


Figure 2. Dorsal and lateral views of the skulls of **A.** *Elseya dentata* (UC0302); **B.** *Myuchelys latisternum* (AM125475) and **C.** *Emydura macquarii* (QM48034).

Habitat. Known from the middle reaches of the rivers they occupy, but greatest abundances for all species of *Myuchelys* occur in the upper reaches and tributaries of the drainage basins they occupy, often above escarpments that exclude other riverine species.

Relationships. Georges and Adams (1992) established the relationships among the four species of *Myuchelys*. Despite being a cryptic species pair, *Myuchelys georgesi* and *M. purvisi* are not sister species, and indeed their common ancestor has all species of *Myuchelys* as its descendants. This suggests that many of the characters jointly possessed by these two species are plesiomorphic for the genus. Relationships between *Myuchelys* and the other short-necked genera are less clear, so we undertook a morphological analysis to complement the prior analyses of molecular data (Georges & Adams, 1992; Georges, et al., 1998). Cladistic analysis of 45 characters (Appendix A) from the extant genera of short-necked Australian chelids yielded a phylogeny with strong bootstrap support for all major nodes (Fig. 3). One tree of 69 transitions in length was shorter than all others, with the next shortest trees (n=3) 71 transitions in length. Genera received at least 74% bootstrap support. The paraphyly of the genus *Elseya*, as previously defined, is clearly evident.

Specimens examined. Abbreviations: AM, Australian Museum; NHM, Natural History Museum (BMNH); NTM, Museum and Art Gallery of the Northern Territory; NWC, National Wildlife Collection; QM, Queensland Museum; UC, University of Canberra; UM, University of Michigan Field Series. *Chelodina expansa*: UC 2099, Albury (36°05'S, 146°55'E); UC 2074, 2190-94, Mungabareena Reserve, Albury (36°06'S, 147°00'E). *Chelodina longicollis*: QM 59266, UC 0199, Hawkesbury River (33°45'S, 150°42'E); QM 59267-68, 59281-2, Jervis Bay (35°08'S, 150°42'E); QM 59274, UC 0134, 0164, 0169, Canberra (35°17'S, 149°08'E); UC 0166, Oasis Creek, Dubbo (32°15'S, 148°36'E); UC 0174, Mumbar, Near Rockhampton (23°23'S, 150°31'E). *Chelodina colliei*: QM 59272-73, 59283, Perth (31°56'S, 115°50'E); UC 0161-63 Perth, (31°56'S, 115°50'E). *Elseya albagula*: QM 48012, 48046, Burnett River, near Gayndah (25°37'S, 151°37'E). QM 47987, 47998, 48002, 48010, Dawson River, Theodore (24°57'S, 150°05'E); AM 123067, Grey's Waterhole, Burnett River (25°32'S, 151°39'E); UC 0305-06 Mary River. *Elseya branderhorsti*: UC 0334, Maurauke River, Irian Jaya. *Elseya dentata*: AM 72692-94, 72934-46, 73346, 79160, Bullo River at crossing of Katherine-Kununurra Road (15°42'S, 129°38'E); NTM 17201, 17205-06, 17210, UC 0309-19, 0328, Douglas River (13°47'S, 131°17'E); *Elseya dentata* [var. South Alligator, sensu Georges & Adams, 1992;1996]: UC 0304, Corroboree Billabong, Mary River; NWC 0531, Deaf Adder Creek (13°04'S, 132°58'); AM 128001-04, Magela Creek; NTM 13985, Pul Pul Billabong,

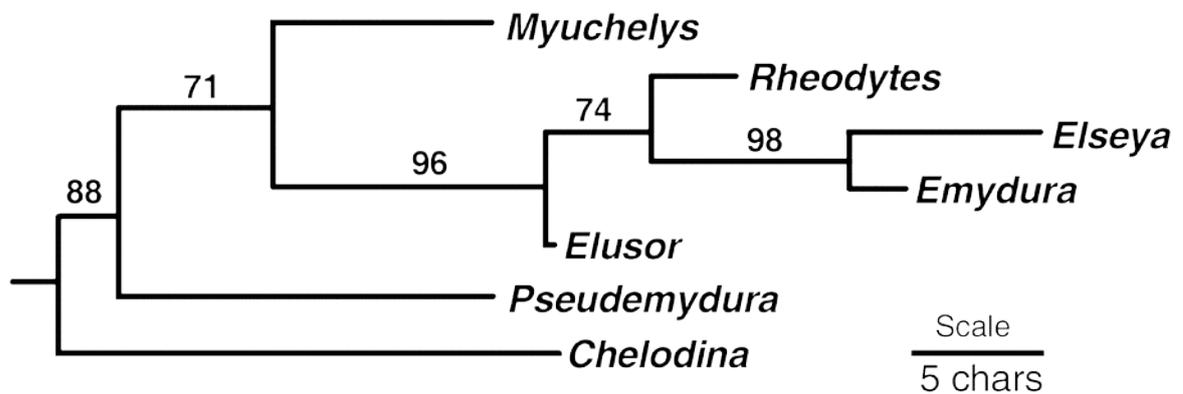


Figure 3. A phylogeny for the extant genera of the Australian short-necked Chelidae generated using PAUP* (v64d) as the single most parsimonious tree from the character data presented in Table 1. Values on the branches are bootstrap percentages—nodes for which values exceed 70% are considered robust. *Phrynops* was used as the outgroup taxon. Note that the genus *Elseya*, as defined prior to this paper (i.e. *Elseya* + *Myuchelys*), was clearly paraphyletic.

South Alligator River (13°34'S, 132°35'); NTM 13512, South Alligator River (13°30'S, 132°28'). *Elseya dentata* [var. Johnstone, sensu Georges & Adams, 1992;1996]: QM 48068, Hartley Creek (15°46'S, 145°19'E); QM 48060, near Cairns (16°55'S, 145°46'E); QM 48059, 48064-65, South Johnstone River (17°38'S, 145°05'E). *Elseya irwini* NWC 0520, Townsville (19°16'S, 146°49'E); *Elseya lavarackorum* QM 47908, 47911, 48547, 48564, Elizabeth Gorge, Bowthorn Station (18°13'S, 138°2'E); QM 31939, 31942, 31944, 31946-47, 31949-50, 31952, Gregory River, Riversliegh Station, north of Mt Isa (19°02'S, 138°45'E); UC 0201, QM 48544, Lawn Hill Gorge (18°46'S, 138°25'E); QM 46284 Lawn Hill National Park (18°35'S, 138°35'E). *Elseya novaeguineae*: AM 42662, 125038, Sepik River, New Guinea (6°47'S, 146°46'E). *Elusor macrurus*: NHM 1890.2.26.2, UC 170, 184-93, 195-197, 225-229, Mary River, Queensland 26°21'S, 152°41'E. *Emydura macquarii*: UC 176, Hastings River (31°26'S, 152°28'E); UC 2063-73, Mungabareena Reserve, Albury (36°06'S, 147°00'E). *Emydura subglobosa*: UC 389, 391, 394-95, Bahunia Springs, Limmen Bight River (16°00'S, 139°05'E); UC 177, Batten Creek, McArthur (15°54'S, 136°40'E); UC 2083-84, Goyder River (12°56'S, 135°01'E); UC 171-72, Gregory River (19°12'S, 137°54'E); UC 2059, 2091, 2095-97, Ooloo Crossing, Daly River (14°04'S, 131°15'E); *Emydura tanybaraga*: UC 2195, Mareeba Wetlands (17°00'S, 145°26'E); UC 464, 468, 469, Ooloo Crossing, Daly River (14°04'S, 131°15'E); *Emydura victoriae*: UC 461, 463, 468, 473, 2055-58, Ooloo Crossing, Daly River (14°04'S, 131°15'E); UC 222, *Myuchelys bellii*: AM123028-29, QM 48028, 48038, billabong on Roumalla Creek, 3 km downstream from bridge at Kingston (30°30'S, 150°07'E); *Myuchelys georgesi*: UM 02016-17, Bellinger River; AM 138387-88, Bellinger River, vicinity of sawmill 1 km from Thora on the Upper Thora Road (30°25'S, 152°46'E); *Myuchelys latisternum*: AM 123037, 123039, Lismore Lake, Lismore, Richmond River Drainage (26°50'S, 153°16'E); UC 470, Richmond River, NSW; AM 125474-75, South Alligator River, Gimbat Station (13°34'S, 132°35'E); QM 48054-55, no data; UC 2094, South Pine River, Bunya crossing (27°21'S, 152°57'E); *Myuchelys purvisi*: QM 59289-90, Barnard River; AM 123040, 123042, Barnard River Natmap 1:250000, Hastings SH56-14 488075 (31°44'S, 151°51'E). *Phrynops geoffroanus*: UC 274, no data, pet trade. *Phrynops hilarii*: UC 330, 336, no data, pet trade. *Phrynops williamsi* UC 298-99, 333, no data, pet trade. *Phrynops tuberosus* UC 328, 332, 337, no data, pet trade. *Batrachemys raniceps*: UC 2043, no data, pet trade. *Pseudemydura umbrina*: UC 178, WAM 29348, Twin Swamps Reserve, Perth. *Rheodytes leukops*: UC 173, 2053, Fitzroy River, Queensland.

Discussion

Evidence for the paraphyletic arrangement of species in the former genus *Elseya* is very strong. It derives from morphological data (McDowell, 1983), electrophoretic data (Georges & Adams, 1992), gene sequencing data (Seddon, et al., 1997; Georges, et al., 1998) and the combined analysis presented in this paper. We have chosen to split the genus *Elseya* to resolve the paraphyly (see Legler & Cann, 1980; Legler, 1981; Georges & Adams, 1992), rather than to combine *Elseya* into an expanded single genus *Emydura* (Gaffney, 1977; McDowell, 1983). The closer affinities of *Elseya dentata* to *Emydura australis* (including *Emydura krefftii* and *Emydura subglobosa*) rather than to *Myuchelys latisternum* (McDowell, 1983) are fully consistent with this new arrangement. It also explains the apparent lack of skull characters that consistently distinguish *Elseya* and *Emydura*, as in making these comparisons (Gaffney, 1977), since Gaffney did not have available skeletal material for *Myuchelys* (then *Elseya latisternum*). The inclusion of *Rheodytes* and *Elusor* in the clade containing *Elseya* and *Myuchelys* (Megirian & Murray, 1999) would preclude the alternative of merging the former *Elseya* with *Emydura* to resolve the paraphyly, as this would require subsuming *Rheodytes* and *Elusor* into *Emydura* also. In our view, this would create a taxonomy that did not adequately represent the variation present in this group, and would not serve the interests of nomenclatural stability by overturning the well-established names *Emydura*, *Elseya*, *Elusor* and *Rheodytes*.

Appendix A. Description of Characters and Character analysis.

Specimens of all species of the *Elseya latisternum* (n = 20) and *Elseya dentata* generic groups (n = 68) defined by Legler (1981) were examined. These were compared with specimens of *Elusor* (n = 20), *Rheodytes* (n = 2), *Emydura* (n = 38, 4 species), *Phrynops/Batrachemys* (n = 10, 5 species), *Pseudemydura* (n = 2) and *Chelodina* (n = 23, 3 species). Character states were assigned and polarized (where possible), and primitive characters assigned the code 0 unless otherwise specified. A character analysis was performed using maximum parsimony (PAUP* version 64d, default settings), with *Phrynops/Batrachemys* as the outgroup (Georges, et al., 1998). Defining characters for each genus were used in the diagnosis. Note that 20 of the 45 characters presented here are autapomorphic and not phylogenetically informative at the genus level. Morphological characters were obtained from the literature or devised in the present study as indicated by an appropriate citation.

Skull characters

1. Alveolar ridge: (medial alveolar ridge between the lingual and maxillary ridges of the triturating surface of the upper jaw): 0—Absent; 1—Present. Absent in all but specialised herbivorous forms; its presence a derived state within the Australian Chelidae.

2. Head shield: 0—Present as a cap on the dorsal surface of the head, with lateral extensions down parietal arch toward the tympanum; 1—Present, but restricted to the dorsal surface of the head; 2—Absent, occasionally present in older individuals but without discrete border or highly fragmented. Cap present in Pelomedusidae and most Chelidae, regarded as primitive, absence a derived loss.

3. Crista supraoccipitalis: 0—not elongated beyond the foramen magnum; 1—elongated beyond the foramen magnum. State 0 the most common state for turtles, considered the primitive state.

4. Parietal arch: 0—Wide; 1—Narrow; 2—Absent. Present in all chelids except *Chelodina*, so complete loss is considered derived. Narrow parietal arch associated with relocation of digastricus masticus muscles of the jaws, derived.

5. Posterior emargination of skull: 0—Present; 1—Absent. Absence is an autapomorphy in *Pseudemydura*, regarded as secondary expansion of the skull roof (Gaffney, 1977).

6. Lingual ridge: 0—narrow not enlarged; 1—enlarged to form crushing plates; 2—enlarged and serrated for shearing plates. Simple narrow structure of triturating surfaces of the jaw sheath, primitive; specialisation for crushing or shearing, derived.

- 7. Medial symphysis of lower jaw:** 0—rami not fused; 1—rami fused to form single unit. Most turtles have a sutural surface between the rami of the lower jaw, primitive; fusion derived.
- 8. Rhamphotheca of upper jaw:** 0—thin, without modification; 1—thickened and enlarged to form a crushing plate. Simple narrow structure of triturating surfaces of the jaw sheath, primitive; specialisation for crushing or shearing, derived. Functionally correlated to Character 6, but not always coincident states.
- 9. Vomer:** 0—contacts pterygoids; 1—does not contact pterygoids. Exclusion of vomer-ptyerygoid contact and medial contact between the pterygoids, derived based on conditions in outgroup taxa.
- 10. Anterior process of frontal** (Gaffney, 1977): 0—present; 1—absent. Absence in *Pseudemydura*, a derived autapomorphy.
- 11. Nasals** (Gaffney, 1977): 0—not completely separated by frontal process; 1—completely separated. Complete separation of nasals, derived synapomorphy for *Chelodina*.
- 12. Prefrontals** (Gaffney, 1977): 0—not exposed along dorsal margin of apertura narium externa; 1 exposed. *Chelus* has character state 1, but Gaffney (Gaffney, 1977) also considers it as being narrowly present for *Chelodina*, hence we include it here. Functionally correlated to presence/ absence and form of nasals, so no characters defined for nasals.
- 13. Frontals** (Gaffney, 1977): 0—not fused, 1—fused. Well defined synapomorphy for *Chelodina*, fusion is considered derived.
- 14. Dorsal portion of postorbital** (Gaffney, 1977): 0—small; 1—large. Broad ventrolateral expansion of postorbital a defined autapomorphy for *Pseudemydura*.
- 15. Dorsal portion of parietal** (Gaffney, 1977): 0—covers little of adductor fossa; 1—covers central area of adductor fossa; 2—broadly covers adductor fossa; 3 absent, does not cover adductor fossa. Functionally correlated with character 24, but not always coincident states.
- 16. Supraoccipita- parietal contact:** 0 narrow, 1—broad. Expansion of the supraoccipital an autapomorphy in *Pseudemydura* (but see Gaffney, 1977)
- 17. Quadrate-parietal contact** (Gaffney, 1977): 0—absent; 1—present. Quadrate excluded from parietal, derived autapomorphy in *Pseudemydura*.
- 18. Dorsal horizontal portion of supraoccipital** (Gaffney, 1977): 0—not expanded; 1—broadly expanded. Autapomorphy for *Pseudemydura*, forming part of expanded roofing of skull.
- 19. Medial portions of jugal and postorbital** (Gaffney, 1977): 0—not facing more laterally than posteriorly; 1—facing more laterally than posteriorly. Complex homology, depends on degree of flattening of skull. State 1 present in *Phrynops*, *Chelus* and the *Chelodina expansa*

group, to a lesser degree in *Hydromedusa*. We agree with Gaffney on the polarity, present only in species with strike-and-gape behaviour.

20. Dorsal processes of exoccipitals (Gaffney, 1977): 0—do not meet above the foramen magnum; 1—meet above the foramen magnum. In most turtles the exoccipitals fail to meet above the foramen magnum, primitive state for the Chelidae.

21. Quadrate basisphenoid contact: 0—absent; 1—present. In most chelid turtles the basisphenoid and quadrate are separated on the ventral surface by the prootic; in *Chelodina*, the basisphenoid extends laterally, anterior to the foramen posterior canalis caracoti interni, to meet the quadrate; derived.

22. Symphyseal hook (Gaffney, 1977). 0—absent; 1 present. Most short necked species in Australia have a pronounced symphyseal hook, with the exception of *Pseudemydura*. Absent in the South American forms, derived.

23. Prearticular separates coronoid and splenial (Burbidge, et al., 1974; Gaffney, 1977): 0—absent; 1—present. In all turtles that retain the splenial, including fossils, the coronoid and splenial have an extensive contact; State 1 autapomorphic for *Pseudemydura*. Splenial is usually absent in Rheodytes (Legler & Cann, 1980), scored as 0.

24. Temporal emargination: 0—emargination minor, not extending deeply into parietal; 1 parietal is significantly narrowed.

Shell characters

Anterior Bridge Struts

25. Contact with Pleural 1 (Thomson, et al., 1997): 0—posterior edge of bridge-carapace suture runs parallel and adjacent to rib-gomphosis of pleural one; 1—posterior edge of suture contacts rib-gomphosis at anterior end, set at a forward divergent angle between 15 and 50 degrees. Angle most pronounced in *Emydura*, least in *Rheodytes*. Bridge strut parallel to the rib-gomphosis in almost all turtles, even many Cryptodires, State 1 derived.

26. Bridge suture shape (Thomson, et al., 1997): 0—anterior and posterior edges of bridge-carapace suture parallel or closely so, with prominent suture surface between them, no medial constriction. 1—anterior and posterior edges of bridge-carapace suture diverge from their point of congruence closest to the vertebral column, widest extent of suture distal to vertebral column, no medial constriction; 2—bridge-carapace suture expanded for full length, more so at extremes, obvious medial constriction; 3—bridge-carapace suture narrows from widest point proximal to vertebral column, constricts completely to form a ridge confluent with edge formed by ventral suture of peripheral bones. One of the most difficult characters to polarise.

Primitive state shared by most chelids and pelomedusids that are unmodified in this region (by plastral hinges).

Rib/Gomphosis of Pleural 1

27. Rotation of Rib/Gomphosis (Thomson, et al., 1997): 0—ventral surface of distal extent of rib/gomphosis rotated obliquely to face ventrally but with posterior inflection; 1—rib/gomphosis shows no such torsion distally. Rotation of the gomphosis is found in almost all chelids, primitive. Functionally it would appear to have strengthened the juncture of the first pleural to the peripherals in this region. It also allows for kinesis and is necessary if that were present. Only *Pseudemydura* has mild plastral kinesis.

Dorsal characters

28. Relative width of Vertebral 1 (Gaffney, 1977, Thomson, et al., 1997): 0—first vertebral scute wider than second and third; 1—first three vertebral scutes equal or sub-equal in width. Gaffney (Gaffney, 1977) identified the wider first scute as primitive, possibly secondarily derived in *Pseudemydura*.

29. Cervical scute (Gaffney, 1977; Legler & Cann, 1980; Thomson, et al., 1997): 0—cervical scute typically present; 1—cervical scute typically absent. This character has been well analyzed and the presence of this scute is clearly primitive for turtles.

Posterior internal carapace characters

30. Carapace pelvis suture (Thomson & Mackness, 1999): 0—ilium sutures to pleurals 7 and 8 and pygal; 1—ilium sutures to pleural 8 and pygal only, but directly adjacent to the suture between pleurals 7 and 8; 2—ilium sutures to pleural 8 and pygal only but widely separated from suture between the pleurals 7 and 8. Most chelids examined possess State 0, primitive, including the outgroups *Phrynops/Batrachemys* and other South American Chelids.

31. Location of rib gomphosis of Pleural 5: 0—inserts between peripherals 7 and 8; 1—inserts into middle of peripheral 7; 2—inserts into peripheral 6: Minor differences in the location of the gomphosis between pleural 5 and the peripherals have been found. These are probably correlated to differences in shell length ratios. State 0 present in the majority of species, many of which are not closely related, primitive.

32. Exposed neural bones present (contiguous series): 0—Present, 1—Absent. Thomson and Georges Thomson & Georges, 1996 demonstrated that neural bones are present in a reduced form in all chelids. This explains their occasional appearance in species that do not generally have a contiguous series of neurals, particularly in older animals. This is an ontogenetic condition and its occurrence is more or less correlated to the thickness of the shell. Some species normally have a large exposed series of neurals – *Chelodina oblonga* (Burbidge et al., 1974); *Myuchelys purvisi* (Thomson & Georges, 1996) and *Chelodina*

burrungandjii (Thomson, et al., 2000). In the *Chelodina* this is associated with the expansion of the rib heads to make room for enlarged musculature, hence is considered derived. In *M. purvisi* this is considered a retained primitive condition.

33. Intergular scute (Gaffney, 1977): 0—intergular large extends between and separates the humerals, 1—intergular small does not separate the humerals. In most chelids, the intergular scute is small and extends back to only partially separate the humeral scutes, primitive condition. In the derived state, intergular scute large, completely separates the humerals and separates the anterior of the pectoral scutes.

34. Gular scutes (Gaffney, 1977): 0—separated by intergular; 1—contact each other excluding intergular from anterior edge. A well defined synapomorphy for the *Chelodina*, useful for the identification of fossil *Chelodina* (Gaffney, 1981 Thomson, 2000).

35. Anterior plastron lobe: 0—large, squared at anterior; 1—small, narrow, tapered at anterior. In most chelids the anterior plastron is square in general shape, primitive; in *Emydura* and *Elseya* the anterior is tapered, derived.

36. Generalised shell shape 0—dorso-ventrally flattened; 1—high domed. In most chelids the shell is flattened. Other characters

37. Number of clawed toes (manus) (Gaffney, 1977): 0—five; 1—four. Primitive state for number of toes on the manus of most tetrapods 5; hence 4 derived.

38. Cervical vertebrae length (Gaffney, 1977): 0—same length as thoracic vertebrae or shorter, 1 longer than the thoracic vertebrae. Elongation of the cervical vertebrae considered derived.

39. Atlas-axis complex structure (Williams, 1950). 0—not fused to single unit; 1—fused to single unit. In the primitive state the atlas-axis complex consists of a number of separate units held together by ligaments and cartilage; in the derived state this complex fuses into a single inseparable bony structure, e.g. *Chelodina*.

40. Skin contact with carapace: 0—skin of ventral surface of carapace does not extend to anterior margin in cervical P1 region; 1—skin extends to approach anterior margin. In most turtles there is a gap between the skin carapace contact at the anterior and the anterior margin, primitive.

41. Hyoids: 0—hyoid complex small; 1—hyoid complex large. Expansion of the hyoid structure is found in turtles that employ the suck and gape feeding strategy, derived.

42. Neck tubercles: 0—present, large and cornified; 1—absent or small, not cornified. Pelomedusids, South American Chelids, *Chelonia*, many fossil taxa have large scales on the head and neck that are fully cornified, primitive.

- 43. Allozyme AK-1** (Georges & Adams, 1992). 0-a, 1-b. Unordered.
- 44. Allozyme AK-2** (Georges & Adams, 1992). 0-a, 1-e. Unordered.
- 45. Allozyme Glo-1** (Georges & Adams, 1992). 0-b, 1-a. Unordered.

Chapter 8: Synopsis

During the course of this study into the relationships of the species in the genus *Elseya*, I made many nomenclatural and taxonomic changes. This resulted from greater understanding and re-evaluation of the importance of certain characters, including use of molecular data, in polarizing and understanding the evolution of characters. I have also integrated fossils into the taxonomy of the genus *Elseya*.

In some cases it was necessary to make a detailed analysis of particular characters. For example, the analysis of a single character, that of neural bones in chelid turtles, (Chapter 2) occupied an entire chapter. Several attempts had been made by previous authors to understand the neural bone character state in turtles in general (Pritchard, 1988) and specifically in chelids (Rhodin and Mittermeier, 1977). What these studies were not able to show and what was brought out in my study, was that all of the turtles I examined possess neural bones, whether or not they are visible at the carapace surface. Their retention as sub-surface elements was demonstrated by doing cross-sections, and knowledge of this sub-surface retention provided more feasible explanations of distribution of the surface expression of this character among species. This was an important discovery, leading to further research, yet to be published (Thomson et al., in prep.) into this complex multi-state character which clearly can now be better polarized and used in phylogenetic analysis. Forthcoming work on the fossil turtles of Tasmania and Queensland and of South America will benefit from this under-utilised and previously misunderstood character.

The generic re-assignment (to *Elseya*) and recognition as a living species of the fossil *Emydura lavarackorum* (White and Archer, 1994) presented in Chapter 3 was the first time that a fossil chelid turtle had been fully integrated into a workable phylogeny of the living species. New characters were presented for the first time in this chapter, characters of broader utility, and it was the first time that the post-cranium was utilized to diagnose chelid genera. The structure of the anterior bridge strut has become a useful diagnostic character, extended to the long necked genus *Chelodina* (Thomson, 2000b; Thomson et al. 2000; McCord and Thomson, 2002) and soon to be further extended to the South American species (Thomson et al. in prep). The work in this particular chapter received public attention (Discover Magazine – Zimmer, 1997).

Much of the work leading up to my thesis relied on cranial characters. For example the landmark studies of Eugene Gaffney (1977; 1981) rested largely on cranial characters. Post cranial morphology was a poorly studied and almost absent feature in turtle systematics. Very

few characters had been developed and those that were had not been adequately studied to rule out convergence or homoplasy more generally. In this thesis, of particular value was the recognition of post-cranial character states of taxonomic significance allowing for the delineation of a number of fossil and extant taxa at the species level, including the species *Chelodina burrungandjii* (Thomson et al. 2000) and *Flaviemys purvisi* (Wells and Wellington, 1985); in the latter case, Le et al. (2013) used these characters in their diagnosis of their new genus *Flaviemys*. Considerable attention was paid to a series of characters around the anterior bridge strut; the form of the suture, the angles and the relationship of the 2nd rib to this structure (Thomson et al. 1997). This and the relationship of the ileum to the pleurals provided a useful series of characters at both generic and species level (Thomson and Mackness, 1999) for identifying fossil species to genus. Three fossil taxa in *Elseya* were re-assessed or described using these characters – *Elseya lavarackorum* (Thomson et al. 1997), *Elseya nadibajagu* (Thomson and Mackness, 1999) and *Elseya uberrima* (Thomson, 2000a). Synonymies and apomorphic based analysis has allowed these fossils to be used in calibration techniques associated with molecular phylogenies (Le et al. 2013; Todd et al. 2013b; Georges et al. 2014).

Whereas Chapter 3 described the bridge strut morphology in the genera of chelids, Chapter 4 focussed on the alignment and character states of the pelvis. These new characters, along with the characters in the previous chapter, were used to define and name the new species *Elseya nadibajagu* (Thomson and Mackness, 1999) and to determine its affinities within the Queensland clade of the *Elseya* and more broadly I provided data to support splitting the species *Elseya dentata* into three species, bringing to finality the long held view that *Elseya dentata* was a species complex (Legler, 1981; Georges and Adams, 1992; 1994). One of these species, *Elseya irwini*, had been named by John Cann (1997b).

Part of delineating and diagnosing the species in the genus was revision of those species already described. A number of previously described species, including from taxa outside *Elseya* and outside the scope of this thesis – *Chelodina canni* (McCord and Thomson, 2002), *Chelodina burrungandjii* (Thomson et al. 2000), and the fossil species *Rheodytes devisi* (Thomson, 2000a), were described, synonymized or resurrected to in some cases correct taxonomic errors from the past, in others, revise the taxonomy as new evidence came to light. One character in particular required attention. The alveolar ridge has been underplayed in revisions of the short-necked turtles of Australasia (Goode, 1967), leading to considerable confusion. My work shows the alveolar ridge to be a defining character of the genus *Elseya* with all members having the character at some level of development, in some

cases (*Elseya novaeguineae*), only on the underlying bones. The structure could be further sub-divided into both an alveolar and lingual ridge (Thomson et al. 2006) and the degree to which these two morphological features are present, absent or a combination of both is species-specific in *Elseya*. A revised synonymy for the species *Elseya dentata* (Gray, 1863) was developed, and has now been adopted by the IUCN TFTSG Checklist (2014). In this way my definition of what this species represents, and its revised distribution, is now recognized in the literature. Another group at issue were the fossils described by C. W. de Vis. These included, among others, the fossil *Elseya uberrima* (de Vis, 1897). In Chapter 5, four species were synonymized under one, and the genus *Pelocomastes* (de Vis, 1897) was declared available and a junior synonym of *Elseya*, representing the Queensland clade of the *Elseya* (Thomson, 2000a).

Other revisions included the examination of the names from Wells and Wellington (1985) which required detailed nomenclatural analysis of the many issues arising from this self-published document. Several names from the paper were rejected as *nomen nudum* under Article 13.1 and 13.2 of the ICZN Code, other names were accepted and validated, some were accepted but synonymized (Iverson et al. 2001). The species names deemed unavailable were *Elseya sterling*; *Chelymys windorah*; *Tropicochelymys insularis* and *Chelodina rankini*. All four of these taxa have since been renamed by various workers (Cann, 1997b; McCord and Thomson, 2002; Cann et al. 2003; McCord et al. 2003). The names deemed to be available and validated were *Macrochelodina* (currently a subgenus of *Chelodina* sensu Georges and Thomson, 2010) and *Elseya purvisi* (currently in the genus *Flaviemys*).

Clarification of the existing nomenclature allowed focus to shift to describing new taxa. In Chapter 6, a new living species was described, *Elseya albagula* (Thomson et al. 2006). The genus *Elseya* as defined at the start of this study contained three poorly defined species (*Elseya dentata*, *Elseya novaeguineae* and *Elseya latisternum*). By the end of this study four species had been removed from *Elseya*, with approximately ten species still in the genus. This work is unfinished, as a number of *Elseya* are still to be described. Most important is the description of a new species of *Elseya* from New Guinea (Thomson and Georges, in prep.), awaiting the final collection of the holotype. This work will not only name a new species but apply names to the three clades in the genus *Elseya* as subgenera. A further species to be described is one from the South Alligator (*Elseya* sp. aff. *dentata* [Magela] of Georges and Adams, 1992; Thomson and Georges, in prep.). There are also two new species of *Elseya* from Queensland to be described, which will benefit from the foundation laid in this thesis.

A major difficulty for the genus *Elseya* (Legler, 1981; Georges and Adams, 1992; and confirmed in this study) was its paraphyly – the common ancestor of the *Elseya* as defined at the time of my thesis work, had *Emydura* among its descendents. A new genus was erected, as presented in Chapter 7, to resolve this paraphyly, *Myuchelys* (Thomson and Georges, 2009), in which four species were placed; *Myuchelys latisternum*; *Myuchelys georgesi*; *Myuchelys bellii*; and *Myuchelys purvisi*. Since this time *M. purvisi* was placed in a new genus *Flaviemys* by Le et al. (2013).

An interim culmination of all the information from this study was presented in two papers. A book chapter in Vertebrate Zoogeography of Australia (Georges and Thomson, 2006) was a summation of the paleozoogeographic knowledge of the time with respect to turtles. A second paper was a complete synonymy and keys to the turtles of Australia and New Guinea (Georges and Thomson, 2010). It examined all names, showed complete synonymies and presented field keys for these species. This work has been utilized heavily by Cogger (2014) and the IUCN TTWG Checklist for Living Turtles (2014). The Australasian and South American chelids remain in need of further review. There are undescribed species both in Australia and South America, and many fossils that have been misidentified to genus, and await formal description. The Chelidae is one of the largest turtle families, with some 60 species currently recognised. It is easily comparable to the Trionichidae or the Emydidae for variety and numbers of taxa. The work continues.

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Appendix A. Nomenclatural Changes since the publications in this thesis.

Nomenclatural changes post-publication follow: Turtle Taxonomy Working Group [van Dijk, P.P., Iverson, J.B., Rhodin, A.G.J., Shaffer, H.B., and Bour, R.]. 2014. Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. *Chelonian Research Monographs* 5(7):000.329–479, doi:10.3854/crm.5.000.checklist.v7.2014.

Aspideretes hurum = *Nilssonina hurum*: the genus *Aspideretes* was synonymized with *Nilssonina* (Engstrom et al. 2004).

Bataguridae = Geomydidae: the family Bataguridae was re-arranged due to significant molecular findings; it was deemed a junior synonym of Geomydidae (van Dijk et al. 2012).

Chelidae subfamilies: Chelinae; Hydromedusinae; Chelodinae. Three subfamilies in this Family are now recognized; Chelinae and Hydromedusinae from South America and Chelodinae for the Australasian species (van Dijk et al. 2012).

The following groups in *Chelodina* were long recognized as being distinctive (Burbidge et al. 1974), they are now recognized as subgenera (Georges and Thomson, 2010).

Chelodina longicollis group / *Chelodina* A = *Chelodina* (*Chelodina*)

Chelodina expansa group / *Chelodina* B = *Chelodina* (*Macrochelodina*)

Chelodina oblonga group / *Chelodina* C = *Chelodina* (*Macrodiremys*)

Within the *Chelodina* a major issue in the nomenclature of the Northern Snake-neck turtle and the South Western Snake-neck turtle was identified (Thomson, 2000b) and eventually resolved, it required the switching of some of the names in this genus (van Dijk et al. 2012; 2014).

Chelodina oblonga = *Chelodina* (*Macrodiremys*) *colliei*

Chelodina rugosa = *Chelodina* (*Macrochelodina*) *oblonga*

Chelodina siebenrocki = *Chelodina* (*Macrochelodina*) *oblonga*

The following species of *Chelodina* have had minor changes to their nomenclature due to the recognition of subgenera (Georges and Thomson, 2010; van Dijk et al. 2012; 2014).

Chelodina alanruxi = *Chelodina (Macrochelodina) alanruxi*

Chelodina expansa = *Chelodina (Macrochelodina) expansa*

Chelodina insculpta = *Chelodina (Macrochelodina) insculpta*

Chelodina longicollis = *Chelodina (Chelodina) longicollis*

Chelodina novaeguineae = *Chelodina (Chelodina) novaeguineae*

Elseya latisternum = *Myuchelys latisternum*

Elseya novaeguineae = *Elseya schultzei*: note: *E. novaeguineae* is a valid species but the specimens examined in this study belong to the taxon *Elseya schultzei* which has since been removed from synonymy)

As noted in Chapter 7 a new genus for the *Elseya latisternum* group was erected. Older papers were using the existing nomenclature at the time. They also prior to the recognition of species in this genus by other workers were using non nomenclatural identifiers from Georges and Adams (1992). The genus *Myuchelys* has also subsequently been split. All current nomenclature for this group is below.

Elseya latisternum = *Myuchelys latisternum*

Elseya sp. aff. *latisternum* (Bellinger River, N.S.W.) = *Myuchelys georgesi*

Elseya sp. aff. *E. latisternum* (Gwyder) = *Myuchelys bellii*

Elseya sp. aff. *latisternum* (Manning River, N.S.W) = *Flaviemys purvisi*

Note on *Elseya* subgroups. The sub groups of the *Elseya* have been somewhat recognized by the Turtle Taxonomy working group. However there are three not two. Since the papers in this thesis were published it has been determined that the *Elseya novaeguineae* complex comprises three species one of which is unnamed at this point, *Elseya novaeguineae* and *Elseya schultzei* being the other two (Thomson and Georges, in prep.). This group is to be given sub-generic status but needs to be named. The other two groups already have names but

require those names to be properly allocated. *Elseya* sensu stricto and hence sub-genus *Elseya* contains *Elseya dentata*, *Elseya branderhorsti* and the yet to be named species from the South Alligator. The Queensland *Elseya* from this paper will be given the sub-genus name *Pelocomastes*, a name to be resurrected from the synonymy of *Elseya*. It contains *Elseya lavarackorum*, *Elseya albagula*, *Elseya irwini*, and a recently discovered species from the Daintree, not examined here. The members of *Elseya* have gone through a large revision, much of it in this thesis. Nomenclatural changes are as follows.

Elseya sp. aff. *E. dentata* (Burnett) = *Elseya albagula*

Elseya sp. aff. *E. lavarackorum* (Burnett) = *Elseya albagula*

Elseya sp. aff. *E. dentata* (Johnstone) = *Elseya irwini* (most recent studies refutes the distinction of this taxa from *Elseya irwini*)

Elseya sp. aff. *E. lavarackorum* (Johnstone) = *Elseya irwini*

The following *Emydura* species have had nomenclatural changes.

Emydura sp. aff. *E. victoriae* (Daly Mission) = *Emydura tanybaraga*

Emydura sp. aff. *krefftii* (Fraser Island) = *Emydura macquarii nigra*

Emydura sp. aff. *subglobosa* (Sleisbeck) = *Emydura subglobosa worrelli*