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The Australian gulf snapping turtle *Elseya lavarackorum* (Testudines: Chelidae) revisited—Is the late Pleistocene fossil species extant?

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Abstract

Disagreement exists on the taxonomic identity of the extant populations of the Australian *Elseya* referred to in 1992 as the gulf *Elseya* (= *Elseya* sp. aff. *dentata* [Nicholson]). The extant form has since 1997 been considered conspecific with the late Pleistocene fossil *Elseya lavarackorum* (White and Archer, 1994). Recently it has been considered a new species, *Elseya oneiros* Joseph-Ouni et al., 2020, conspecific with another fossil found in the same site and stratum as *Elseya lavarackorum*. Here we re-examine the fossil material and reassess the characters used by previous authors in an attempt to decide the issue. We find that the anterior bridge suture with the carapace of the fossil *Elseya lavarackorum* is associated with extensive and prominent plastral elements, which has led to misinterpretation of characters associated with this structure. We furthermore show that interindividual variation in sulci patterns is so great as to render them of little taxonomic value. On the basis of (a) deviation of the anterior shape of the carapace from ovoid such that, in aged individuals, the most anterior point of the carapace occurs at marginal scutes M2 (a resultant nuchal bay occurs in such individuals); (b) the typical absence of a cervical scute; (c) no evidence of a medial constriction in the anterior bridge strut suture; and (d) absence of evidence of any other informative variation of taxonomic value; we conclude that the decision to consider the late Pleistocene (ca 23 kyr old) fossil and the extant *Elseya* sp. aff. *dentata* [Nicholson] as *Elseya lavarackorum* (White and Archer, 1994) as conspecific should stand.

Keywords

Introduction

In May 1984, exploration of eroded fluviatile deposits exposed in the catchment of the Gregory River on Riversleigh Station, north-western Queensland, revealed several sites that produced fossil vertebrates. One of these, known as Terrace Site (Davis and Archer 1997), produced abundant remains of chelid turtles, including the

somewhat crushed but nearly complete plastron, partial carapace and partial pelvic remains of a large chelid turtle (UNSW AR14547 = QM F24121, White and Archer 1994). The fossil specimen was diagnosed by the first vertebral scute being much wider than the second; vertebral scutes 2 and 3 being rectangular, longer than wide, with only small projections into the costal scute junctions; a relatively wide intergular scute on the plastron that deeply divides the humeral scutes; a humeral-pectoral seam that is sigmoidal rather than straight; and internal attributes of the girdles and their articulation. White and Archer (1994) noted the absence of the cervical scute and a leading edge of the carapace that does not curve posteriorly until the suture between marginal scute 2 and 3. They compared the attributes of the fossil specimen to those of a range of short-necked Australian chelid taxa for which information was available at the time (*Elseya dentata*, *Emydura krefftii*, *Emydura macquarii*, *Rheodytes leukops*, *Elusor macrurus* and *Pseudemydura umbrina*). White and Archer (1994) noted some of the attributes of the fossil more closely resemble those of the long-necked chelids (*Chelodina*), but on the basis of other characters, assigned the fossil to the genus *Emydura*. They formally described the fossil as *Emydura lavarackorum* in honour of Sue and Jim Lavarack who collected the holotype.

Thomson et al. (1997) re-evaluated the fossil *Emydura lavarackorum* in the context of additional information and a broader representation of extant Australian chelid turtles. They more tightly defined the character states associated with the anterior bridge suture with the carapace. On the basis of this character (distinctly different in the fossil from that of *Emydura*), the width of vertebral scute 1 relative to that of vertebrals 2 and 3, and the absence of a cervical scute (absent only as a rare variant in *Emydura*), they reassigned *Emydura lavarackorum* to the genus *Elseya*. This reassignment has been widely accepted (Cogger 2018).

Referring to the recessed nuchal region, Thomson et al. (1997) assigned *Elseya lavarackorum* to the subgenus *Pelocomastes*. This character state has been variously described as: "the leading edge of the carapace is almost straight and does not curve posteriorly until the suture line between the second and third marginal scutes" (White and Archer 1994); "an indentation of the carapace margin in the area of the cervical cleft and first marginal scutes" (Thomson et al. 1997); "anterior carapace expanded, anterior extent of second marginal scute as great or greater than that of first marginal scute in adults" (Georges and Thomson 2010); or nuchal emargination (Joseph-Ouni et al. 2022). This character state is not observed in *Elseya* (*Elseya*) and is ontogenetically variable in *Elseya* (*Pelocomaste*s) becoming evident in only the largest, presumably oldest, specimens.

Thomson et al. (1997) went further in assigning extant populations of an undescribed form of *Elseya* in the Gregory-Nicholson drainage to the fossil holotype. Genetic analyses had established the gulf snapping turtle (*Elseya* sp. aff. *dentata* [Nicholson]) as a distinct species with affinities to the Queensland clade of *Elseya* (Georges and Adams 1992, 1996) (now *E. lavarackorum*, *E. irwini*, *E.*

albagula, subgenus *Pelocomastes*). Thomson et al. (1997) concluded from the size of the fossil specimen and its strongly embossed, rounded peripheral bones in the region adjacent to the bridge, that the fossil represented an aged individual. This is an important consideration in making comparisons with other material, because of the substantial ontogenetic variation in many diagnostic characters. Taking this into consideration, the observation that the fossil specimen did not differ in any substantial character states from the extant populations of the Gregory-Nicholson drainage and the young age of the fossil (est. late Pleistocene, ca 23,900 years BP, Davis and Archer 1997), led Thomson et al. (1997) to assign the extant populations to *Elseya lavarackorum* (White and Archer, 1994).

In a recent paper, Joseph-Ouni et al. (2022) revisited the assignment of *Elseya lavarackorum* to the Queensland clade of *Elseya* (subgenus *Pelocomastes*). They also revisited the proposition of Thomson et al. (1997) that the fossil and extant *Elseya* sp. (aff. *dentata* [Nicholson] = *Elseya lavarackorum* sensu Thomson et al. 1997) belonged to the same chronospecies. In challenging both propositions, Joseph-Ouni et al. (2022) drew upon and strengthened an analysis presented earlier by Joseph-Ouni et al. (2020) in a publication promulgated outside the normal channels of scientific discourse (via The Turtle and Tortoise Preservation Group, https://www.ttpg.org, last accessed 31-Dec-22). They instead argued that the chelid turtle fossils found in the deposit with *Elseya lavarackorum* represent two species, *Elseya* (*Elseya*) *lavarackorum* (White and Archer, 1994) and *Elseya* (*Pelocomastes*) *oneiros* Joseph-Ouni et al., 2020, the former extinct and the latter comprising a new chronospecies that includes the extant form *Elseya* sp. aff. *dentata* [Nicholson].

Characterization of morphological variation in the shells of extant *Elseya* can provide a baseline for interpretation of the character states of fossil specimens. However, other studies of this type serve to highlight the difficulties inherent in recognizing and accommodating intraspecific diversity in the fossil record (Vitek 2018; Guerrero and Pérez-García 2021; Joyce et al. 2022; Liaw and Tsai 2022). This challenge becomes particularly acute when relatively few fossil specimens are available. Differences between the sexes where the sexes are often unidentified in fossil material, and ontogenetic variation whereby large specimens in the fossil record represent an extension of the allometric trajectory present in available extant specimens, present particular difficulties for interpretation. Conspecificity of young fossils and extant populations is equally challenging to establish or refute, but it is not particularly uncommon to find reference to late Pleistocene fossils considered to be also represented by extant populations of the same species (Guilday et al. 1978; Willis 1990; Archer et al. 2019; Liaw and Tsai 2022). The question is one of whether the young fossil and the extant populations are on the same evolutionary trajectory, requiring phylogenetic judgement, and if they are, whether the fossil and extant forms show sufficient morphological divergence as to be considered separate chronospecies, which requires a subjective judgement (Dzik 1990; Futuyma 2005).

In this paper, we confirm that the affinities of *Elseya lavarackorum* lie with the subgenus *Pelocomastes*, not with the subgenus *Elseya* (Joseph-Ouni et al. 2020, 2022). We question the taxonomic value of characters used by Joseph-Ouni et al. and argue that the evidence they present is not sufficient to establish that *Elseya lavarackorum* (represented by the focal fossil) and *Elseya oneiros* (represented by a fossil from the same Riversleigh Terrace Site stratum) are distinct evolutionary species (separate and diagnosable lineages – sensu Futuyma 2005). We further argue that the evidence and argument presented by Joseph-Ouni et al. (2022) is not sufficient to establish that the extant *Elseya* sp. aff. *dentata* [Nicholson] and the young fossil *Elseya lavarackorum* (approx. 23.9 Ka BP) are distinct enough to refute the hypothesis of their both being the same species (i.e. chronospecies, sensu Dzik 1983, 1990). We conclude that the name *Elseya lavarackorum* (White and Archer, 1994) should stand for the extant gulf snapping turtle.

Methods

Specimens examined

We examined the fossil holotype (QM F24121) for *Elseya lavarackorum* (White and Archer, 1994) catalogued and housed at the University of New South Wales, which comprised a partial carapace (Fig. 1), a partial but near complete plastron (Fig. 2) and several isolated fragments that have not been assembled; an additional fossil partial plastron (QMF30817) (Fig. 3) from the same strata at the Riversleigh Terrace Site referred to *Elseya lavarackorum* by Thomson et al. (1997) by association; and a third near complete fossil plastron (QMF30818) (Fig. 4) also from the same strata at the Riversleigh Terrace Site referred to *Elseya lavarackorum* by Thomson et al. (1997) by association and to *Elseya oneiros* by Joseph-Ouni et al. (2022). Note that specimens QM F24121, QM F30817 and QM F30818 have been accessioned and catalogued by the Queensland Museum but not yet housed there. Instead, they have been catalogued and housed by the University of New South Wales (UNSW), where they were viewed by us. The fossil holotype (QM F24121) is catalogued with UNSW as AR14547; QM F30817 and QM F30818 are catalogued with UNSW as QMF30817 and QMF30818 respectively. The fossil material will ultimately come to be housed at the Queensland Museum. To avoid confusion and to reflect current holdings, we hereafter refer to the fossils as UNSW QMF24121 (the holotype), QMF30817 and QMF30818. A full list of specimens examined is provided in Appendix 1.

We also examined high quality photographs of extant specimens provided to us by the co-authors of Joseph-Ouni et al. (2022) and others (Supplementary Materials) to assess interindividual variability in characters based on scutellation, where relevant.

Phylogenetic Analysis

A total of 106 characters scored for 24 taxa were used for phylogenetic analysis using Maximum Parsimony as implemented in PAUP Version 4.0a (build 169) for 32-bit Microsoft Windows (built on Feb 10 2021 at 22: 12: 44). A heuristic search was undertaken, with MAXTREES set to 40,000. A consensus of 10,236 equally parsimonious trees (length 153) was obtained using Majority Rule (> 0.5), and consensus for nodes is indicated on the Fig. 8 and Fig. S1. Bootstrap support values were based on 1,000 replicates, again obtained using PAUP (Supplementary Material 3), and indicated on Fig. 8 and Fig. S1. Synapomorphies were obtained using TNT 1.5 (Goloboff et al. 2008) and added to the tree in Fig. S1. All characters were unordered, of equal weight, and the tree-bisection-reconnection (TBR) branch swapping algorithm was used. Fossils were included as independent taxa. Fossils were coded only on those characters present on the type specimen regardless of other existing material, as recommended by Parham et al. (2015). *Podocnemis sextuberculata* was used as the outgroup. The data matrix of characters by taxa is available in Table S1.

Results

Character Analysis

Shell terminology follows that of Zangerl (1969) with the exception of our reference to costal scutes and pleural bones (following Pritchard and Trebbau 1984). Terminology of the elements of the shell associated with the bridge follows that of Thomson et al. (1997) and Thomson and Mackness (1999). For consistency with this earlier work to which we continually reference, we refer to the anterior bridge strut which is also referred to as the axillary buttress or the axillary hyoplastral buttress (Joseph-Ouni et al. 2022). Strictly, the anterior bridge strut is a structural complex comprising the axillary buttress of the plastron, the associated pleural bones and peripherals of the carapace, and associated sutures (Thomson et al. 1997). It is a key structural element that affords stability to the shell and most developed in river turtles. We pay particular attention to the position and shape of the suture of the anterior bridge strut with the internal face of the carapace – hereafter the bridge strut suture. Analysis of available characters relevant to the assignment of the fossil chelid turtles of the late Pleistocene Terrace Site fossils at Riversleigh has been undertaken by the original authors White and Archer (1994) and subsequently by Scott Thomson and his co-authors (Thomson et al. 1997; Thomson 2000; Thomson et al. 2015; Thomson and Georges 2009, 2016).

Bridge strut suture

The Anterior Bridge Strut Suture, or axillary hyoplastral buttress suture of Joseph-Ouni et al. 2022, is a charac-
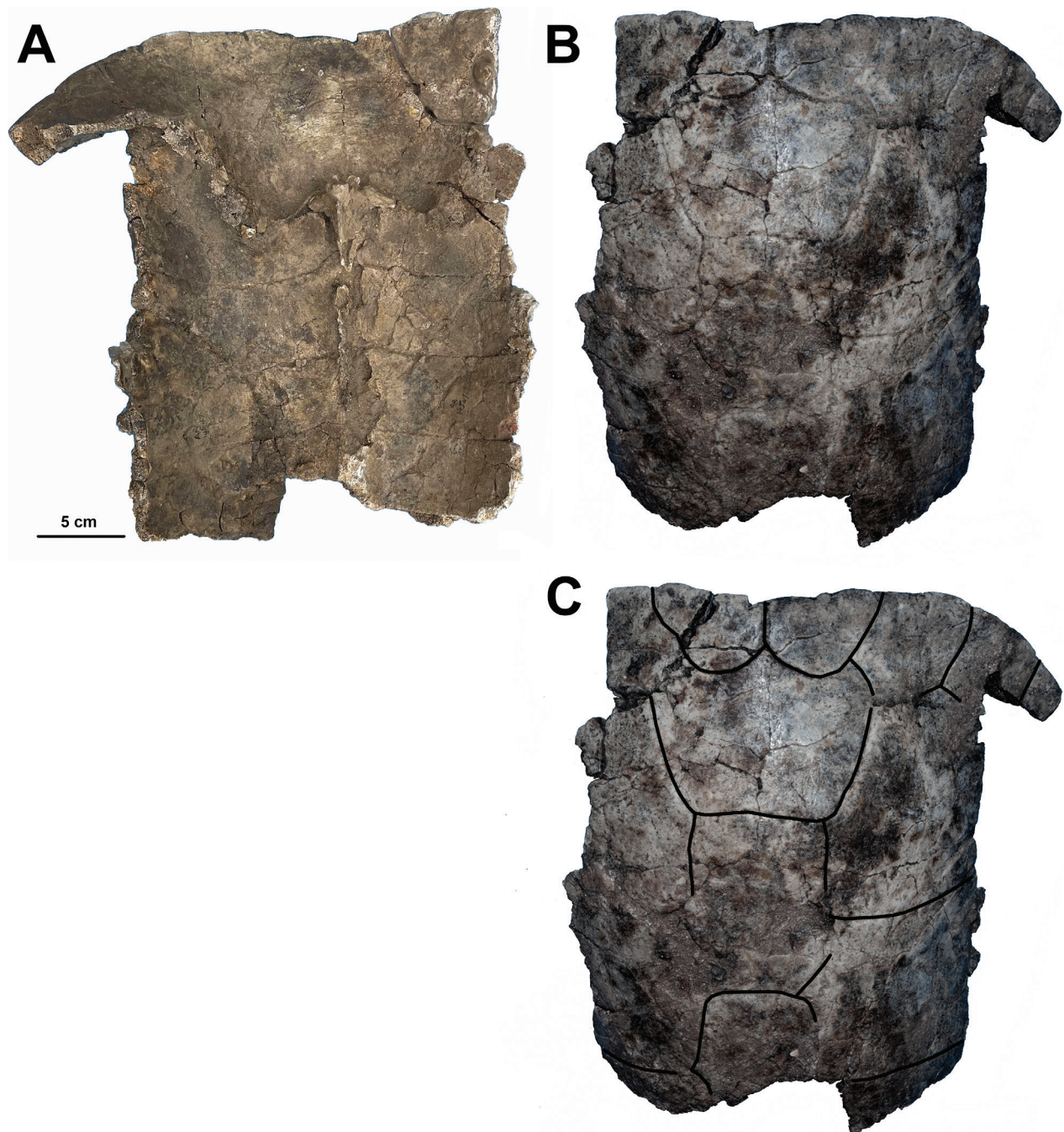
Figure 1. Carapace of the fossil holotype of *Elseya lavarackorum* (White and Archer, 1994) (QMF24121). **A** Dorsal view; **B** ventral view; **C** dorsal view with sulci marked where they can reliably be discerned (solid lines). Note the points of most anterior extent establishing the existence of a nuchal bay.

ter central to the re-evaluation of the affinities and therefore identity of the *Elseya lavarackorum* fossils by Joseph-Ouni et al. (2022). It is a character established as taxonomically informative at the level of genus and subgenus in the Australian Chelidae (Thomson et al. 1997; Thomson 2000; Thomson et al. 2015; Thomson and Georges 2009, 2016). A key element of the case made by Joseph-Ouni et al. (2022) rests on their observation that the terminal end of the bridge strut suture is club shaped, and that the medial region of the suture is constricted. The fossil carapace of UNSW QMF24121, when viewed from the ventral (internal) perspective, includes the region of the anterior plastron bridge strut suture (Figs 1A, 5). The

magnitude of the angle of the bridge strut suture relative to the rib element of pleural bone 1 is a feature that clearly places the fossil UNSW QMF24121 in one of the genera *Elseya* or *Emydura* to the exclusion of *Myuchelys*, *Rheodytes*, *Elusor* and *Pseudemydura* (Thomson et al. 1997, their Figures 2 and 3). The bridge strut suture on the left side (turtle's right side) of the pictured fossil (Fig. 5) is relatively intact; on the right side it appears to have been obliterated during mineralization (arrow (a), Fig. 5A). One reason why the one bridge strut suture was preserved is that the connection between plastral elements of the bridge and carapace appear to have been largely intact *in situ*, preventing it from becoming obliterated as did the
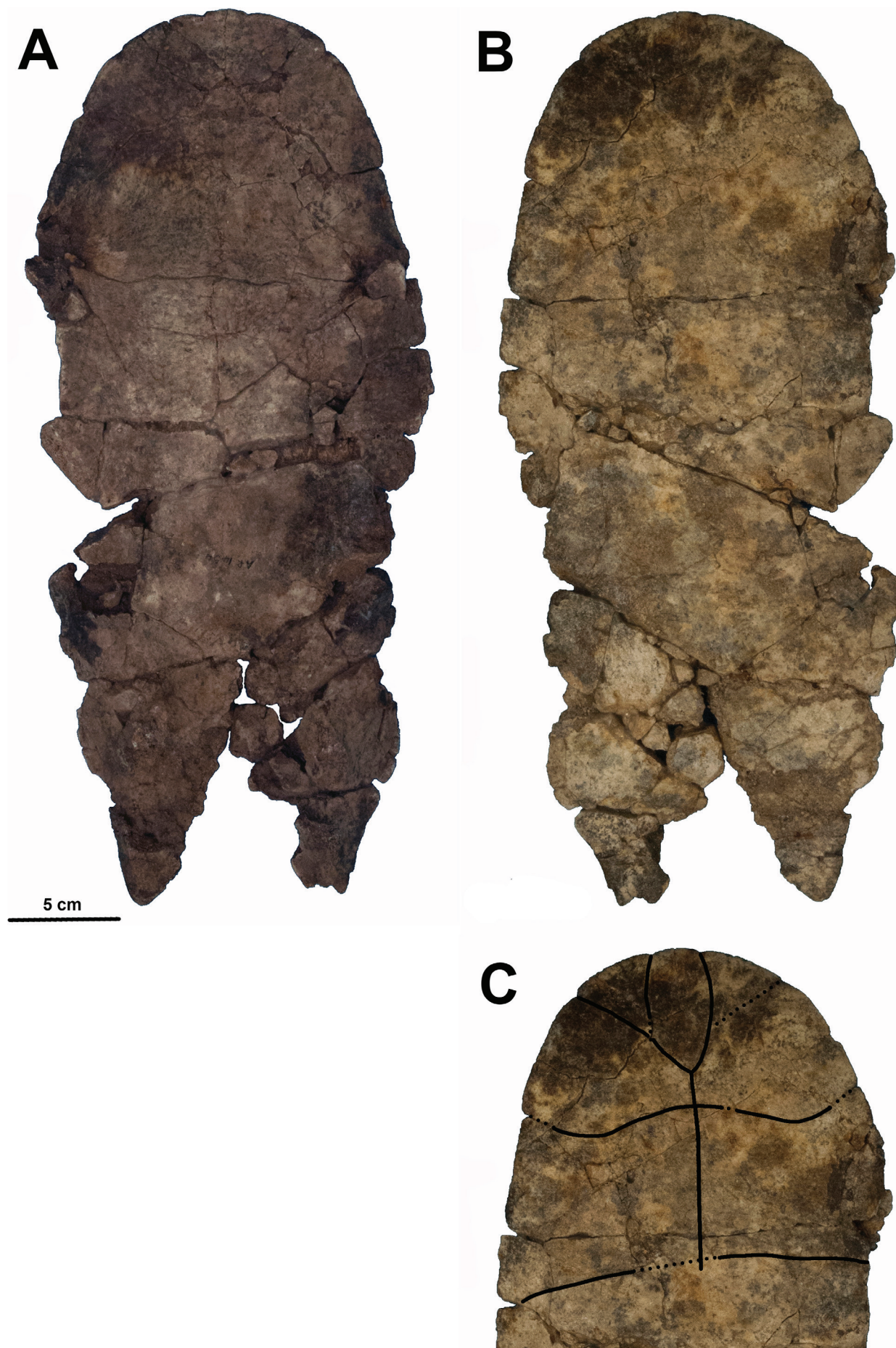
Figure 2. Plastron of the fossil holotype of *Elseya lavarackorum* (White and Archer, 1994) (QMF24121). **A** Dorsal view; **B** ventral view; **C** partial ventral view with sulci marked where they can reliably be discerned (solid lines).
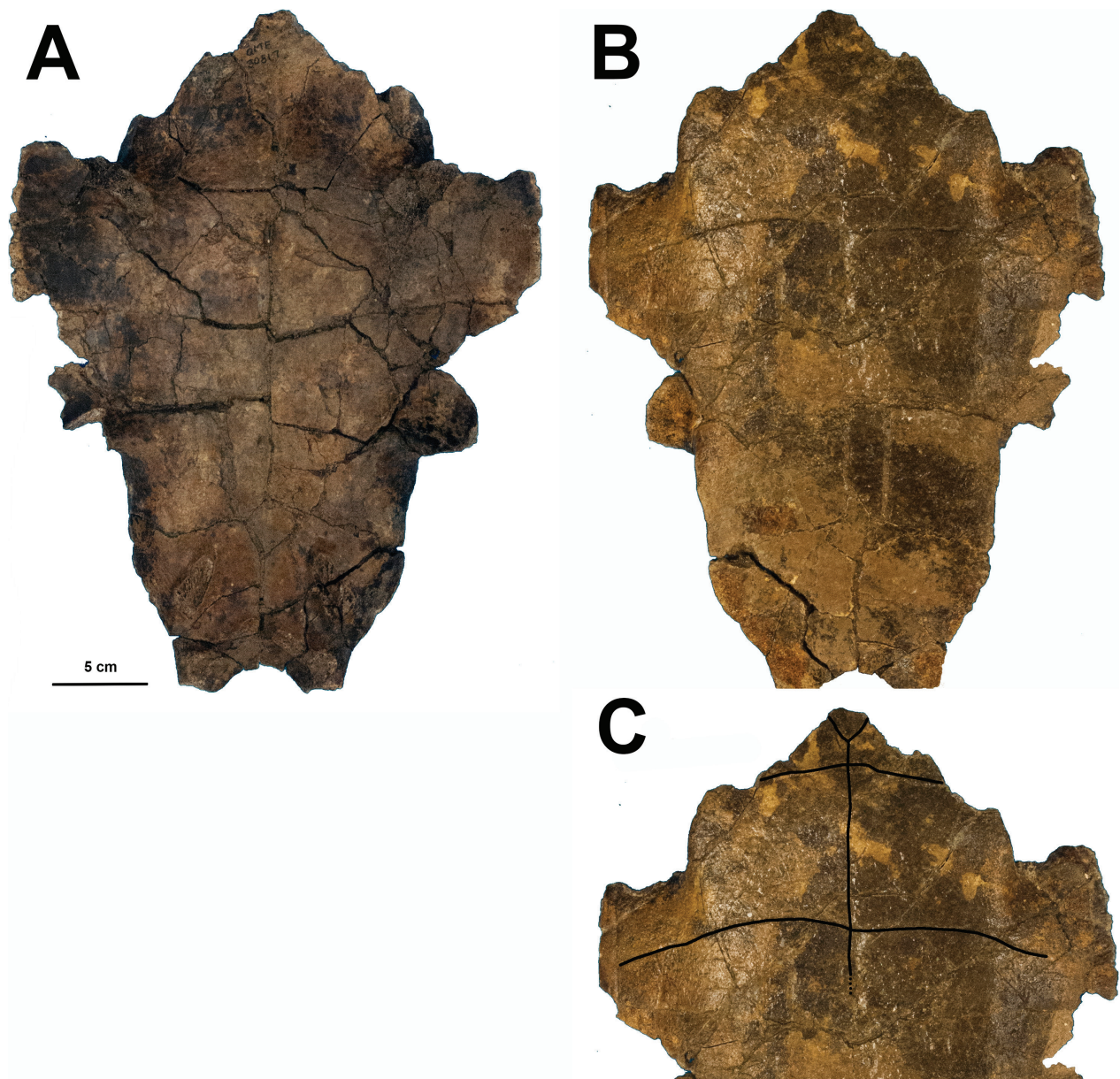
Figure 3. Incomplete plastron of the fossil referred to *Elseya lavarackorum* (White and Archer, 1994) by Thomson et al. (1997) by association (QMF30317). **A** ventral view; **B** dorsal view; **C** partial ventral view with sulci marked where they can reliably be discerned (solid lines). The fossil is not sufficiently complete to obtain usable character states relevant to our qualitative discussion.

other suture. The connection between plastron and carapace was physically broken as the fossil was removed for collection. This is evident as sections of freshly broken matrix (arrows (b), (c) and (e), Fig. 5A).

Fragments of the hyoplastron of UNSW QMF24121 remain associated with the bridge strut suture (arrows (c), (e) and (f), Fig. 5A) which complicates identifying the sutural boundary. These plastral remnants extend laterally at the basal and terminal ends of the bridge strut suture to form shelves that obscure the boundary of the bridge strut suture ((c) and (e) of Fig. 5A, 5B). The terminal shelf (e) extends laterally 3.8 mm and the basal shelf (c) extends 4.3 mm. There is also a terminal overhang of 3.3 mm in plastral elements in the vicinity of (f). Joseph-Ouni et al. (2022) have variously included or excluded this plastral material (their Plate 2A, reproduced as Fig. 5C) in their interpretation of the shape of

the anterior bridge strut suture. This renders that interpretation invalid. For example, they include all of the terminal shelf in determining the boundary of the bridge strut suture and only a small part of the basal shelf (Fig. 5C). They miss altogether the region of the most terminal element of the bridge strut suture (labelled (f) in Fig. 5A). Their interpretation of the shape of the terminal suture boundary ("terminal bulb") represents the shape of the break between the anterior bridge strut and the embedded residual elements of that strut, not the shape of the anterior bridge strut suture itself. This gives rise to the misinterpretation of an "inflated rounded bulb" (Joseph-Ouni et al. 2022), for which there is clearly no convincing evidence. Nor is there evidence of the severe constriction possessed by *Emydura* nor the mid constriction of the suture characteristic of the subgenus *Elseya* (Thomson et al. 1997). Indeed, the contrary is evident in the width of
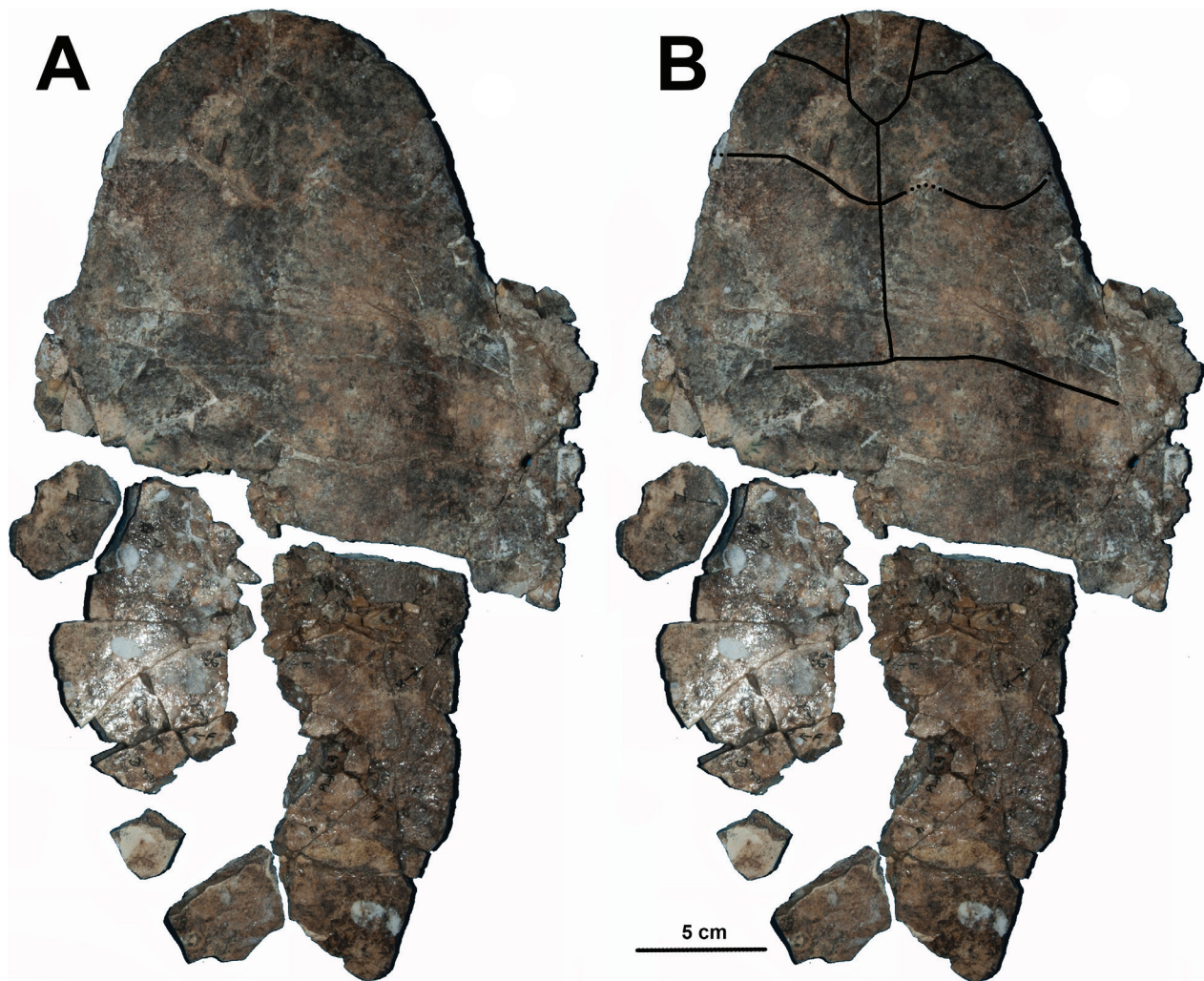
Figure 4. Incomplete plastron of the fossil referred to *Elseya lavarackorum* (White and Archer, 1994) by Thomson et al. (1997) by association (QMF30318). **A** Ventral view; **B** ventral view with sulci marked where they can reliably be discerned (solid lines).

the suture where this can be confidently determined ((d) of Fig. 5A)).

The other two fossils from the Riversleigh Terrace Site (QMF30317, QMF30318) contemporary with the *Elseya lavarackorum* fossil are represented by plastral material only (Figs 3, 4) so that the character state for anterior bridge strut suture cannot be determined.

Nuchal bay

A second character of relevance to the assignment to subgenus of UNSW QMF24121 is the recessed nuchal region of the carapace relative to the adjacent peripheral bones, variously referred to as a nuchal bay, nuchal notch or nuchal emargination (Antunes and de Broin 1988; Gaffney et al. 2006; Brinkman et al. 2008). The ontogenetic extreme state for this character in UNSW QMF24121 and extant members of subgenus *Pelocomastes* (Figs 5A, 6C) has points on the anterior boundaries of marginals M2 as the most anterior points of the carapace, and the carapace does not curve posteriorly until M3. This results in a recessed nuchal region (nuchal bay) evident at marginals M1 and portions of M2. At earlier growth stages,

the anterior peripheral bones are expanded anteriorly and laterally to cause a departure of the shape of the anterior carapace from the typical ovoid shape (Fig. 6A). This then progresses to give a "squared off" anterior to the carapace (Fig. 6). This character state has not been recorded in species of *Elseya* (*Elseya*) regardless of age (see *Elseya* (*Elseya*) *branderhorsti* of Fig. 6A).

The fossil holotype of *Elseya lavarackorum* (UNSW QMF24121) is incomplete, but nevertheless on the right side the most anterior point of the carapace falls on the anterior margin of the Marginal M2. The left M2 is missing so the most anterior point of the remnant carapace on that side falls on the anterior margin of M1. Drawing a line between the two provides a conservative estimate of the presence of a nuchal bay, likely to be more evident had the left M2 been preserved. Thus, the most anterior extent of the carapace of the fossil holotype of *Elseya lavarackorum* lies on the anterior margin of right M2, and a nuchal bay is clearly evident (Fig. 6).

The other two fossils from the Riversleigh Terrace Site (QMF30317, QMF30318) contemporary with the *Elseya lavarackorum* fossil are represented by plastral material only (Figs 3, 4) so that the character state for nuchal bay cannot be determined.
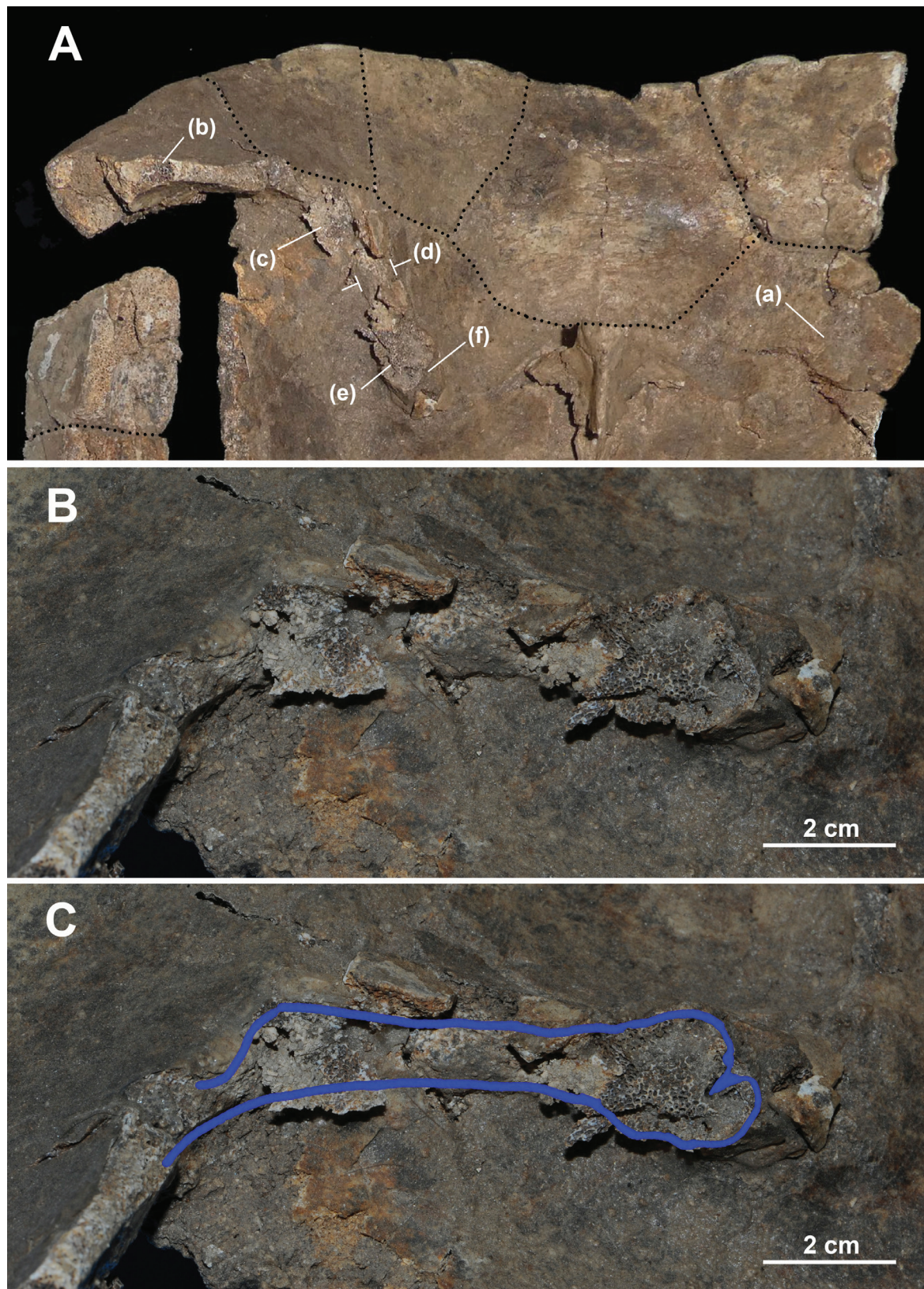
Figure 5. The anterior bridge strut suture between the plastral bridge element and the carapace in the holotype of *Elseya lavarako-rum* (QMF24121). **A** Ventral (internal) view of the carapace showing the strong angle of the anterior bridge strut suture against the rib element of pleural bone 2, and the prominent anterior bridge strut elements still embedded in the suture; **B** an enlarged view of the region of the suture showing more clearly the breaks that were formed when the carapace was separated from the plastron and the resultant overhangs (labelled (c) and (e) in A above); **C** the boundary of the anterior bridge suture as interpreted by Joseph-Ouni et al. (2022). Note that they have selectively excluded and included plastral elements in their boundary definition [(c) and (e) of A]. Note also that major portion of the suture is not included in their interpretation [(f) of A]. Their boundary of the terminal end of the suture represents the boundary of the shape of the break between the anterior bridge strut and the residual elements of that strut embedded in the suture, not the shape of the anterior bridge strut suture.
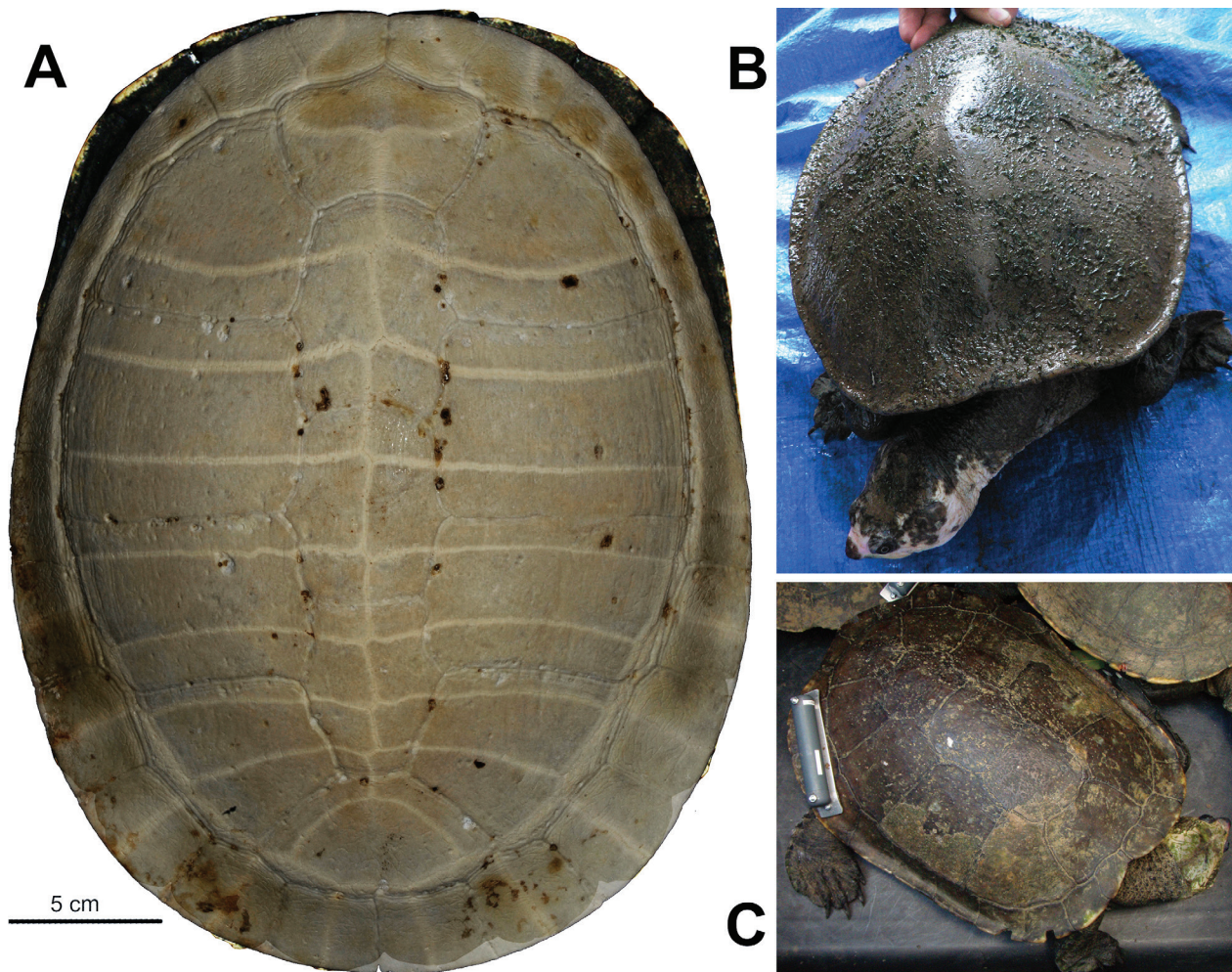
Figure 6. Characterisation of shell shape in species of *Elseya* (*Pelocomastes*). **A** Ovoid shell of *Elseya* (*Elseya*) *branderhorsti* (ANWC R08292) overlaid on the holotype of *Elseya* (*Pelocomastes*) *albagula* (QM 81785) to illustrate the lateral expansion of the anterior peripheral associated with marginal scutes M1 and M2 ("squaring off"). In the largest individuals of *Elseya* (*Pelocomastes*) this expansion leads to the development of a nuchal bay, whereby the most anterior points of the carapace are associated with marginals M2, with marginals M1 recessed to a point at their juncture (in the absence of the cervical), a feature of the fossil holotype of *Elseya lavarackorum*. Scale applies to *Elseya branderhorsti*. **B** Aged specimen of *Elseya* (*Pelocomastes*) *lavarackorum* (Boodjamulla National Park, Qld); **C** Aged specimen of *Elseya* (*Pelocomastes*) *irwini* (Johnstone River, Qld). Photos A: Arthur Georges; B: Alastair Freeman; C: Ivan Lawler.

Scutellation

The fossils of the Riversleigh Terrace Site are unusual in that the scutes of the shell appear to have remained incorporated into the fossils. As a consequence, the bony sutures of the carapace and plastron are less prominent on the surfaces external to the shell, and the sulci are evident as scute junctions rather than indentations in the underlying bone. Joseph-Ouni et al. (2020, 2022) considered a range of characters derived from scute variation. Scutes and their associated sulci provide challenging characters because of high variability among individuals. This presumably arises from underpinning interindividual genetic variation coupled with environmental influences during development (Lynn and Ullrich 1950; Zimm et al. 2017) that often manifests as asymmetry (Cherepanov 2014). For example, a comprehensive survey of scute variants in *Emydura macquarii nigra* found that such variants were present in 28.8% of individuals (n = 670), with 81.8% of

scute additions or deletions occurring in the anterior of the shell (Georges, 1982, reproduced in Supplementary Table S3 and Table S4). As an example of sulci variation that does not involve gain or loss of entire scutes, we examine the character first noted by White and Archer (1994) in their description of the fossil *Elseya lavarackorum* (as *Emydura lavarackorum*), that is, a sigmoidal rather than straight humeral-pectoral seam. This character was redefined and used by Joseph-Ouni et al. (2022) to distinguish *Elseya lavarackorum* from the extant *Elseya* sp. aff. *dentata* [Nicholson]. Thomson et al. (1997) noted this character but did not place particular importance on it as being of taxonomic value. This is for good reason. This character adopts almost all character states in individuals of extant *Elseya lavarackorum* as inter-individual variation (Fig. 7), including the state possessed by the fossil. Furthermore, the states for this highly variable character have a profound effect on other adjacent sulci characters, such as the length of the interhumeral sulcus, and through
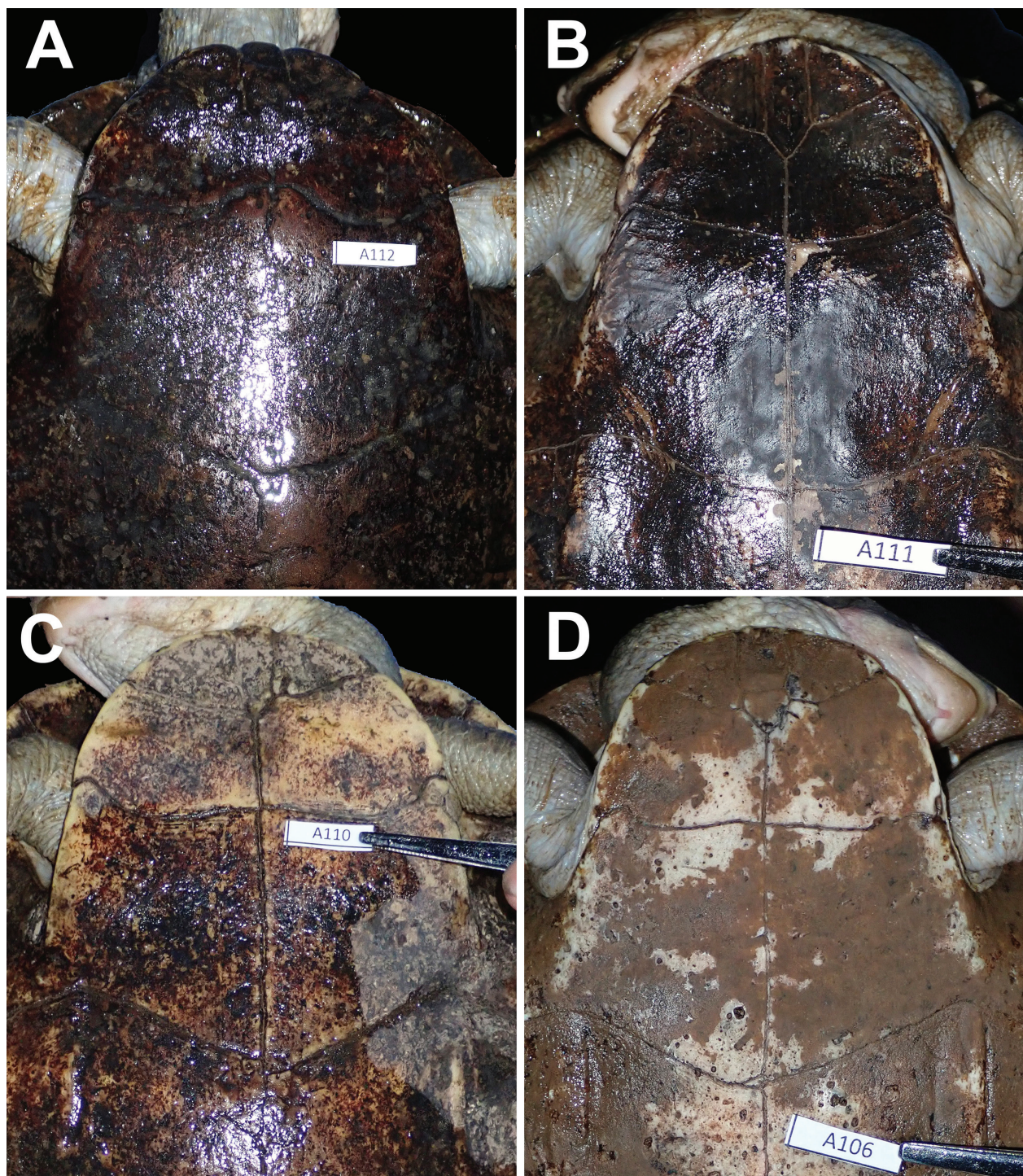
Figure 7. Variation in the humeral-pectoral sulcus in extant *Elseya lavarackorum* from the Roper River, NT. **A** Specimen A112 shows the character state represented by the fossil holotype *Elseya lavarackorum* (sinusiodal sulcus sensu White and Archer 1994); **B** specimen A111 exhibits another variant of the humeral-pectoral sulcus; **C** specimen A110 shows the character state considered important by Joseph-Ouni et al. (2022); **D** specimen A106 shows the character state typical also of *Elseya dentata*. The character state of QMF30818 (inverted sinusoidal cf (a) *lavarakorum*, Fig. 4) is not represented in the specimens we have available. The character is not scorable in the partial plastron of QMF30817 (Fig. 3). This character state will have a substantial influence on the length of the interhumeral sulcus, and thus on all sulci characters that involve this length. Photos: Dion Wedd.

it, the relative penetration of the intergular in separating the humerals.

As an example of variation in a meristic character, the sulci between the first vertebral scute V1 and the first costal scute C1 join to marginal scutes M3 in the *E. oneiros* holotype (QM J47908, arguably a rare aberration) where-as they typically join on each side to marginal scutes M2 in other specimens depicted by Joseph-Ouni et al. (2020) (arguably the typical condition; e.g. their Plate 8d(QM J31946), Plate 12b(E), Plate 12d(QM J77959). In a speci-men of *Elseya dentata* (their Plate 8b(B), the sulcus joins marginal scute 3 on one side and marginal scute 2 on the

other side, indicating that this character is under developmental influence (Cherepanov 2014), presumably from the incubation environment. Morphometric scute characters can show considerable ontogenetic variation, as in the anterior marginal region of *Elseya* (*Pelocomastes*) associated with the formation of the nuchal bay (Fig. 6), so that cross-species comparisons using relatively few individuals of different sizes/ages is problematic.

Furthermore, many of the scute characters of Joseph-Ouni et al. (2020) depend one upon the other, and so cannot be considered independent. In some cases, they are used in part-whole correlation/regression analysis without acknowledgement of the statistical consequences (Davis 1958). The intergular scute of the *Elseya oneiros* holotype is extremely narrow (Plate 10 and Plate 13b of Joseph-Ouni et al. 2020), a second infrequent aberration in this type specimen. This is likely to have consequences for other anterior plastral scute sulci and their measurement.

Other Characters

Joseph-Ouni et al. (2022) identified nine new characters, their characters F–N, that they argue distinguish between *Elseya lavarackorum*, *E. oneiros* and *E. dentata*. In our view these characters suffer from a number of deficiencies. Some are highly variable across taxa, including the three focal taxa (e.g. Character F). Some are profoundly influenced by the misinterpretation of the Anterior Bridge Strut Suture (Fig. 5) (e.g. H, K, L and M). For example, Character M has state M0 under the misinterpretation of the outline of the Anterior Bridge Strut Suture, but M2 if the full extent of the suture is considered. Other characters are likely to be subject to ontogenetic variation as shell shape changes with age (Cadena et al. 2008; Ferreira et al. 2016), a possibility that has not been addressed using an ontogenetic series. Many of their characters are co-dependent. For example, their Characters G, H, J and K and Character A (incorrectly attributed to Thomson et al. 1997) are co-dependent. They are also likely subject to ontogenetic change with change in shell shape with age which dictates that, at the very least, individuals of the same size/age should be compared. None of these characters have been scored across sufficient taxa to make a useful contribution to the phylogeny used to establish the placement of *E. lavarackorum* (Fig. 8).

Phylogeny

Generating a robust phylogeny using a combination of fossil and extant taxa is challenging because the fossils are often partial whereby the matrix of character states (Table S1) is sparse, with many characters unable to be scored. Nevertheless, we were able to generate a phylogeny (Fig. 8, maximum parsimony consensus tree) with clades relevant to the focus of this paper well supported by consensus and bootstrap values (Fig. 8). A clade comprising of species of *Elseya* (*Elseya*) was well supported with 100% consensus and a bootstrap score of 79% (*E. dentata*, *E. flaviventralis*, *E. branderhorsti*), as was its sister clade *Elseya* (*Pelocomastes*) with 100% consensus and a bootstrap score of 84%. Although the internal arrangements were unresolved (a polytomy), the *Pelocomastes* clade comprised the extant *Elseya albagula*, *E. irwini* and *Elseya* sp. aff. *dentata* [Nicholson]. This support for the two clades and the species that make them up is consistent with the results of molecular analyses (Seddon et al. 1997; Georges et al. 1999; Todd et al. 2014). This clade also includes the type species *Pelocomastes uberrima* (de Vis, 1897) and the fossil species *Elseya nadibajagu* Thomson & Mackness, 1999 both previously assigned to this group (Thomson 2000; Thomson et al. 2015). The fossil *Elseya lavarackorum* (QMF24121) and the two other fossils assigned to this species by Thomson et al. (Thomson et al. 1997, QMF30817, 30818) fall within the *Pelocomastes* clade (Fig. 8). The placement of QMF30187 and QMF30818 within the *Pelocomastes* clade was not resolved, and on the basis of this evidence alone they could not be assigned reliably within this subgenus (= *Pelocomastes* sp. incertae cedis). Nor is it possible to refute the proposition that they belong to the taxon *Elseya* (*Pelocomastes*) *lavarackorum*, as proposed by Thomson et al. (1997).

Although not directly relevant to the questions posed in this paper, the phylogeny provides information of broader relevance to chelid phylogeny. Caution is required in the interpretation of the topology, particularly where the support values are low. The three clades of *Elseya* represented as the subgenera are well supported by allozymes (Georges and Adams 1992), mtDNA sequences, nuclear DNA sequences (Seddon et al. 1997; Georges et al. 1999; Todd et al. 2014) and morphology (Thomson and Georges 2009; Thomson et al. 2015 and Fig. 8). The clade *Hanwarachelys* is distinctive, and its affinities have been particularly problematic (Boulenger 1889; Goode 1967; Georges and Thomson 2010). The monophyly of the genus *Elseya* has not been definitively demonstrated and is considered unlikely taken in the context of the genera *Myuchelys* Thomson & Georges, 2009 and *Birlimarr* Megirian & Murray, 1999.

Taxonomy

The lectotype of *Pelocomastes ampla*, type species for *Pelocomastes* is partial and its synonymy with *Chelymys uberrima* (Thomson 2000) was based on their being from the same locality and horizon, and not being able to distinguish them as taxa at the level of species. The name *Pelocomastes* is applied to the clade of Queensland *Elseya* as the oldest available name. This is currently a nomenclatural stable arrangement that could be further consolidated by assigning a neotype for *Pelocomastes ampla* from the same horizon and locality as the lectotype. The most diagnosable fossil candidate for such a neotype is the lectotype of *Chelymys uberrima*. Its se-
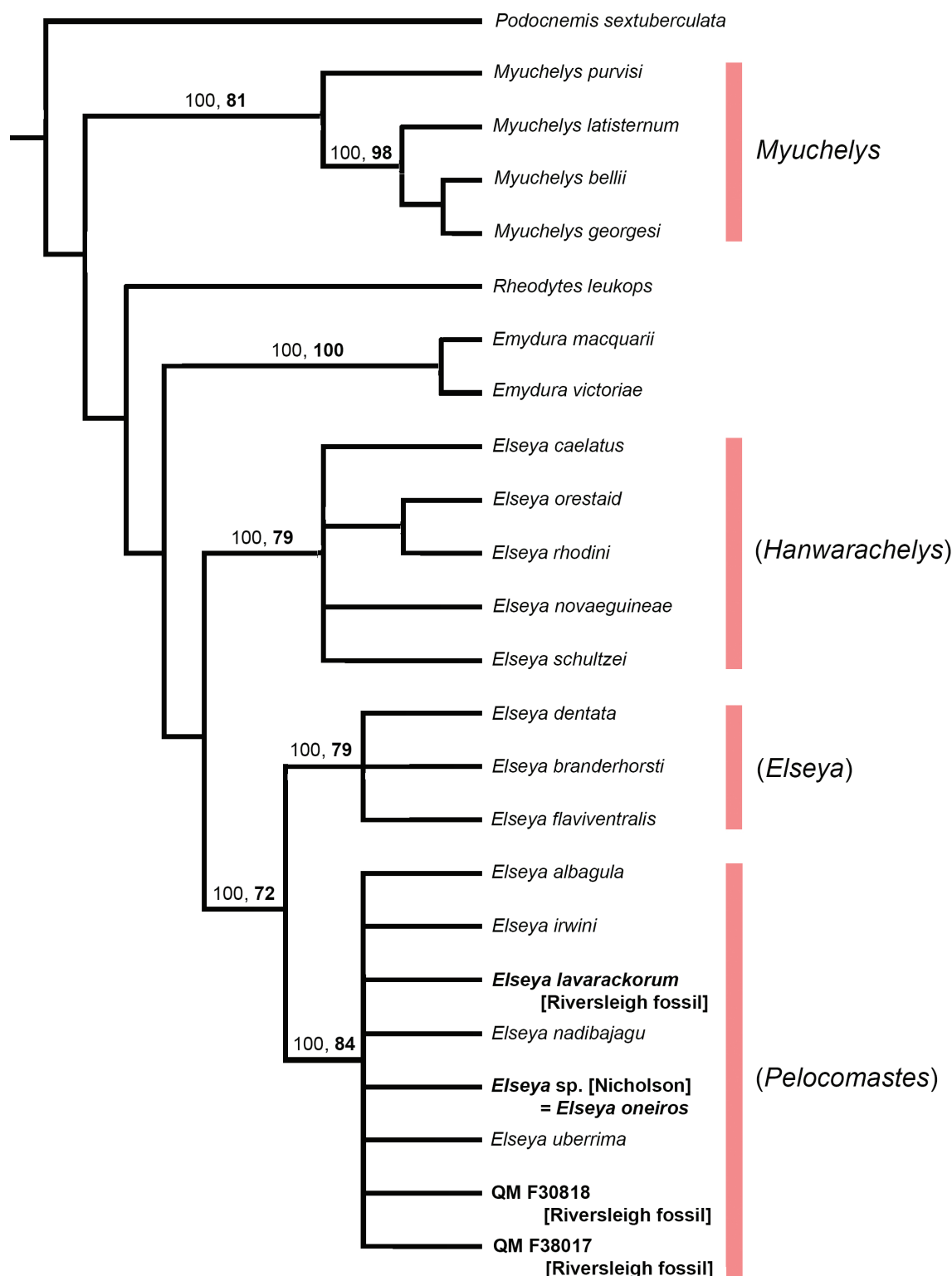
Figure 8. A phylogeny (Majority Rule Consensus Tree, length 153) of 24 extant and fossil species of chelid turtle based on 106 morphological characters (Tables S1 and S2). Pelomedusoid *Podocnemis sextuberculata* was the outgroup taxon. Note that the clades representing subgenera *Elseya* and *Pelocomastes* have high consensus (first value on nodes) and strong bootstrap support (second value on nodes). The fossil material from the Riversleigh Terrace Site and the extant *Elseya* sp. aff. *dentata* [Nicholson] fall in the *Pelocomastes* clade.

lection as a member of the Queensland *Elseya* would achieve stability, avoiding possible challenge to the priority of the names *Chelydera*, *Elusor*, *Myuchelys* or *Rheodytes*, all potentially junior synonyms to *Pelocomastes* should it ever be elevated to genus. The type exists and is available, so if one were to pursue the option of setting a neotype for *Pelocomastes* (e.g. lectotype of *Chelymys uberrima* which is from the same locality and horizon as *P. ampla*) it would require a decision of the International Commission of Zoological Nomenclature (ICZN).

Subfamily: Chelodininae Baur, 1893 sensu Zhang et al. (2017)

Genus *Elseya* Gray, 1867

Subgenus: *Elseya* Gray, 1867 sensu Thomson et al. (2015)

Type species. *Chelymys dentata* Gray, 1863 (= *Elseya* (*Elseya*) *dentata* [Gray, 1863] sensu Thomson et al. 2015)

Included species. *Elseya* (*Elseya*) *branderhorsti* (Ouwens, 1911) sensu Thomson et al. (2015), *Elseya* (*Elseya*) *flaviventralis* Thomson & Georges, 2016 sensu Thomson et al. (2015).

Subgenus: *Hanwarachelys* Thomson et al., 2015

Type species. *Platemys novaeguineae* Meyer, 1874 (= *Elseya* (*Hanwarachelys*) *novaeguineae* [Meyer, 1874: 128] sensu Thomson et al. 2015).

Included species. *Elseya* (*Hanwarachelys*) *caelatus* Joseph-Ouni & McCord, 2019: 25 sensu Joseph-Ouni and McCord (2019), *Elseya* (*Hanwarachelys*) *orestiad* Joseph-Ouni & McCord, 2019: 47 sensu Joseph-Ouni and McCord (2019), *Elseya* (*Hanwarachelys*) *schultzei* (Vogt, 1911: 410) sensu Thomson et al. (2015) and *Elseya* (*Hanwarachelys*) *rhodini* Thomson et al., 2015: 69 sensu Thomson et al. (2015).

Subgenus: *Pelocomastes* de Vis, 1897 sensu Thomson et al. (2015)

Type species. *Pelocomastes ampla* (= *Elseya* [*Pelocomastes*] *uberrima* de Vis, 1897 sensu Thomson 2000, Thomson et al. 2015).

Included species. *Elseya* (*Pelocomastes*) *albagula* Thomson, Georges & Limpus, 2006 sensu Thomson et al. (2015), *Elseya* (*Pelocomastes*) *irwini* Cann, 1996 sensu Thomson et al. (2015), *Elseya* (*Pelocomastes*) *lavarackorum* (White & Archer, 1994: 159) sensu Thomson et al. (2015) and *Elseya* (*Pelocomastes*) *nadibajagu* Thomson & Mackness, 1999) sensu Thomson et al. (2015).

Field identification. Although many of the external characters are highly variable and thus not diagnostic when considered individually, it is possible to provide guidance for the identification of extant *Elseya* (*Elseya*) *dentata* and *Elseya* (*Pelocomastes*) *lavarackorum*. This is particularly important where they occur in sympatry (e.g. the Roper River, NT, Georges et al. 2021). The typical features that distinguish the two are shown in Figs S2–S4. *Elseya* (*Pelocomastes*) can be distinguished from *Elseya*

(*Elseya*) by the presence of extensive lingual ridges in addition to the alveolar ridges on the rhamphotheca; an intergular scute that moderately separates the humerals, at most half (half or more in *Elseya* (*Elseya*); serration of the rear of the carapace that extends into adulthood; and departure from the classical ovoid shape of the carapace (typified by *Elseya* (*Elseya*), Fig. 6) by squaring off of the anterior carapace in *Elseya* (*Pelocomastes*) leading ultimately to a nuchal bay in the largest, oldest individuals (Fig. 6). *Elseya* (*Pelocomastes*) *lavarackorum* can be further distinguished from *Elseya dentata* by the presence of red flushing on the undersurface of the limbs and on the feet (Fig S3), and the reticulate patterning of the temporal region of the head, fading with age (Fig S3). If genotyping is available (e.g. DArTcap, Guppy et al. 2020), the distinction between the two (and between *Elseya* [*Pelocomastes*] *lavarackorum* and *Elseya* [*Elseya*] *flaviventralis*) is definitive (Georges et al. 2021).

Discussion

We re-examined the fossil material relevant to *Elseya* (*Pelocomastes*) *lavarackorum* (White and Archer, 1994) and considered the interpretation of characters by Joseph-Ouni et al. (2022) in coming to their conclusion that the fossil *Elseya lavarackorum* and the extant *Elseya* sp. aff. *dentata* [Nicholson] (Georges and Adams 1992, 1996) are different species. We question their interpretation of the shape of the anterior bridge strut suture where Joseph-Ouni et al. (2022) state that the axillary buttress (our anterior bridge strut) suture is medially constricted with a bulb terminus that is easily discernible (caption of Plate 4B, Joseph-Ouni et al. 2022). Joseph-Ouni et al. acknowledge that the suture contains substantial embedded plastral elements but did not consider the impact of these elements on the interpretation of the shape of the "terminal bulb". Instead, Joseph-Ouni et al. define the shape of the terminal region of the anterior bridge strut suture as the boundary of the breakage between associated embedded plastral elements and the plastral bridge strut (Fig. 5C). These elements include a substantial shelf that extends 3.8 mm laterally from the bridge strut suture. The boundary of the breakage does not provide an indication of the shape of the terminal end of the anterior bridge strut suture, nor does this "terminal bulb" support the conclusion of a medial constriction. Indeed, we have argued that, on the basis of measurements where the suture is not obscured by embedded plastral elements, there is no evidence of a medial constriction. Indeed, it is probably impossible to make a judgement on the shape of the anterior bridge suture given the degree to which it is obscured by residual plastral elements. We conclude that there is no evidence that the shape of the anterior bridge strut suture in the fossil *Elseya lavarackorum* (UNSW QMF24121) departs in any substantial or demonstrable way from what is observed in extant species of the subgenus *Pelocomastes*. The combined absence of a cervical

scute and presence of a nuchal bay in the fossil *Elseya lavarackorum*, an aged individual, is further confirmation that the fossil lies in the subgenus *Pelocomastes* (rarely, aged individuals of subgenus *Hanwarachelys* can have a recessed cervical scute). The nuchal bay is a shared derived character for *Pelocomastes*. This feature, and the marginal scutes M2 as the most anterior point on the carapace is unique among Australian chelids, restricted to species of subgenus *Pelocomastes* (*E. albagula*, *E. irwini*, *E. lavarackorum*), notwithstanding its ontogenetic variation (present only in the largest, aged individuals).

The analysis of Joseph-Ouni et al. (2020, 2022) relies heavily on the interpretation of scutellation variation. We have shown that considerable inter-individual variation in scutellation (Fig. 7) renders such characters of questionable taxonomic value. The inter-individual variation in scutellation we have identified are examples of the challenges in using scute characters from a single individual (e.g. the *Elseya lavarackorum* fossil) in species assignment. For this reason, we reject the overall selection of scute characters and the analysis of scute character states presented by Joseph-Ouni et al. (2020, 2022) as inconsistent, unreliable and of questionable taxonomic value in resolving the species identity and affinities of the *Elseya lavarackorum* fossil (UNSW QMF24121).

We are not arguing that scute characters are of no value taxonomically. Clearly, the contact or lack of contact of the gular scutes anterior to the intergular is an important diagnostic character at the level of genus in the Australian Chelidae. The numbers of costal and vertebral scutes are important taxonomic characters for the species identification of marine turtles (Wyneken 2001). The issue is to decide which such characters are well-defined and consistent at the level of species taxonomy for the group under scrutiny, and not subject to unacceptable inter-individual variation within putative species. In some cases, ontogenetic variation needs to be considered, such as when a distinction not evident in subadults is diagnostic in adults (e.g. the nuchal bay). Sexual dimorphism is also a source of variation which, if sex is not known as is typically the case with fossils, can generate false distinction between two putative taxa (Bunce et al. 2003). Good taxonomic characters should not be metrically dependent, as is the length of the interhumeral sulcus and the degree of penetration of the intergular to partially separate the humerals. The most valuable scute characters are likely to be those accompanied by a character state shift in the underlying bone elements. We argue that Joseph-Ouni et al. (2022) have not established their sulci characters as well-defined and consistent at the level of species taxonomy, as our examples demonstrate (Fig. 7).

Even given the above caveats, scutellation characters may be informative and form part of the description of the Type material, but not in a diagnostic sense. Scutellation characters can be used to capture differences in the pattern of interindividual variation between putative species that overlap to varying degrees in different putative species using Principal Components Analysis (PCA) or Discriminant Analysis (DFA). This requires capturing a good representation of that interindividual variation for

all taxa under consideration and of course, that is very seldom possible when examining fossil forms; it is certainly not possible to capture interindividual variation in the population from which the fossil *Elseya lavarackorum* (UNSW QMF24121) was drawn, given the limited and incomplete fossil material available. Without available information on interindividual variation in both the fossil putative taxon and the extant putative taxon, it is not possible to assess the level of overlap in morphological space. PCA and DFA require dense data matrices of characters against putative species, seldom achievable when working with incomplete fossil specimens. This is the tyranny of limited fossil material in the context of fossil-extant taxon comparisons. These issues have not been adequately addressed by Joseph-Ouni et al. (2022) in the case they make for overturning the assignment of the extant gulf snapping turtle to *Elseya lavarackorum* (White and Archer, 1994).

Marrying the procedures for defining species based on extant and fossil taxa is challenging (Vitek 2018). The two disciplines, palaeontology and taxonomy of extant forms, work under fundamentally different constraints. In zoology, species are natural units defined on reproductive barriers to gene flow, notwithstanding operational challenges for their delineation. In palaeontology, addition of the time factor requires limits that are subjective and more or less arbitrary, and in any case different from the limits in zoology (Drooger 1954). Vertebrate palaeontology typically works with one or a very few specimens and so is unable to assess characters against a backdrop of inter-individual variation within species. Best practice in describing extant forms draws upon a pool of available specimens for the putative new species and for those against which it is compared to establish a defensible character analysis. Paleontologists have to consider the concept of chronospecies, taxa on the same evolutionary lineage, but separated by time and the accumulation of some morphological change (Dzik 1990; Futuyma 2005). In contrast, species delimitation of extant forms needs to consider time in the form of phylogenetic history of the extant lineage and those closely related to it, but the exercise is largely constrained to a snapshot in time, the present.

The two perspectives come together when considering species delineation of very young fossils and sub-fossils. The fossil material, usually represented by a single specimen or a few specimens, is compared to living forms for which there are abundant data to capture inter-individual variability. Under this framework, there are two ways to argue that the fossil *Elseya lavarackorum* and the extant *Elseya* sp. aff. *dentata* [Nicholson] (Georges and Adams 1992, 1996) are different species (see also steps outlined by Dzik 1990). The first is to demonstrate that the fossil *E. lavarackorum* and the fossil and extant *E. oneiros* are on different evolutionary trajectories. Joseph-Ouni et al. (2020) argue that *E. lavarackorum* is a member of the *Elseya* genus/clade whereas *E. oneiros* is a member of the *Pelocomastes* genus/clade. We argue that the *Elseya lavarackorum* fossil has a clear *Pelocomastes* character that is uniquely present in aged individuals in that sub-

genus. Joseph-Ouni et al. (2020) are correct in noting that this character is variable (it is subject to ontogenetic variation and rarely present in *Elseya albagula*), but incorrect in concluding that it is of no taxonomic value in assigning the fossil to a subgenus. This is a shared derived character state that unites the extant *Pelocomastes* including the fossil *E. lavarackorum*. Our phylogenetic analysis (Fig. 8) places the fossil *E. lavarackorum* clearly within the subgenus *Pelocomastes*. There is therefore no evidence to regard the fossil *E. lavarackorum* and the extant *Elseya* sp. aff. *dentata* [Nicholson] as residing on different evolutionary lineages.

The second way to make a case that the fossil *Elseya lavarackorum* and the extant *Elseya* sp. aff. *dentata* [Nicholson] are different species is to argue that they are chronospecies, that is, that they are on the same evolutionary lineage, with the more recent individuals having diverged sufficiently from the earlier individuals to warrant them being considered as separate species. It is a significant challenge to demonstrate that variations seen between a single ancient fossil and modern-day individuals of the same species are not just a result of natural adaptations within the same species. The fossil that is from late Pleistocene sediments, aged by carbon dating (and companion fossils) at 23.9 Ka BP (+4100–2700) (Davis and Archer 1997). For context, human remains have been discovered and dated in Australia at 62 ± 6 Ka (Thorne et al. 1999). The period of 23.9 Ka BP is arguably too short to support the evolution of two chronospecies, even taking into account the errors in this age determination (Davis and Archer 1997). Joseph-Ouni et al. (2022) have not, on the basis of our analysis, demonstrated that the young fossil *Elseya lavarackorum* and the extant form represent distinct chronospecies.

We argue that Joseph-Ouni et al. (2022) have dismissed characters that are taxonomically of value (e.g. the squaring off of the anterior carapace and ultimately formation of a nuchal bay in aged individuals), have misinterpreted characters (e.g. the bridge strut suture confounded by retained plastral elements), and have selectively placed weight on characters that vary so greatly among individuals as to be of limited value taxonomically for distinguishing species. Their statistical analyses are flawed (e.g. unacknowledged part-whole correlations and functional dependencies among characters) or incomplete (no multivariable analyses). They do not undertake a phylogenetic analysis to ascertain the affinities of the fossil (subgenus *Elseya* or *Pelocomastes*) and in any case, the distribution of character states across their putative taxa is so sparse as to render them uninformative in such a phylogenetic analysis. We therefore argue that there is no foundation in the works of Joseph-Ouni et al. (2020, 2022) for rejecting the proposition that *Elseya lavarackorum* (White and Archer 1994) and the extant *Elseya* sp. aff. *dentata* [Nicholson], separated by only *ca* 23 Kyr, are the same species. To bring this point home, the holotype of *Elseya oneiros* Joseph-Ouni et al., 2020 differs from other individuals of the taxon it represents, *Elseya* sp. aff. *dentata* [Nicholson], in two important respects – the sulci of V1 join with M3 not M2 on each side and the

intergular is exceptionally narrow. Were this specimen a fossil, and were weight placed on sulci characters as have done Joseph-Ouni et al. (2022), this individual would be a new species distinct from the extant *Elseya* sp. aff. *dentata* [Nicholson]. Scute sulci are highly variable among individuals and cannot reliably be used in species delimitation without demonstrating their consistency, especially when the material at hand is a single individual.

We note that Joseph-Ouni et al. (2022) pay particular attention to arguing that Thomson et al. (1997) have not demonstrated the two, *Elseya lavarackorum* and *Elseya* sp. aff. *dentata* [Nicholson] (Georges and Adams 1992, 1996), are the same species. However, Thomson et al. (1997) concluded instead that the differences between the two were not sufficient to reject the proposition that they were the same species. In that paper, we followed a well-established process of viewing conspecificity as the null proposition, to be challenged or otherwise by the publication of defensible evidence and analysis that refutes that null proposition. The onus is on others to demonstrate, through re-examination of the evidence and interpretation of characters relevant to the *Elseya* and related taxa, and the presentation of new defensible characters, that the two represent distinct species. Joseph-Ouni et al. (2022) have not done this.

Conclusion

Based upon our reanalysis of the fossils and associated characters in the extant forms, including those of subgenus *Pelocomastes*, we find that the differences between the fossil *Elseya lavarackorum* (White and Archer, 1994) and *Elseya* sp. aff. *dentata* [Nicholson] (Georges and Adams 1992, 1996) are not sufficient to overturn the current taxonomy that considers the two to be the same species. We consider the assignment of the *Elseya lavarackorum* fossil to the subgenus *Elseya* to be incorrect, and that its affinities lie with the subgenus *Pelocomastes*, so nor is there evidence that the fossil and the extant form are on separate evolutionary trajectories. The young age of the fossil is relevant (approx. 23.9 Ka BP). We place *Elseya oneiros* (Joseph-Ouni et al., 2020) as a junior synonym to *Elseya lavarackorum* (White and Archer, 1994).

Author Contributions

Acknowledgements

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Appendix 1

Specimens examined

Abbreviations: AM, Australian Museum; AMNH, American Museum of Natural History, New York; ANWC, Australian National Wildlife Collection, Canberra; NHM, Natural History Museum of London; MTD, Museum für Tierkunde, Senckenberg Dresden; ZMB, Museum für Naturkunde Berlin, MV, Museum of Victoria; NTM, Museums and Art Galleries of the Northern Territory; PNGM, Papua New Guinea National Museum; QM, Queensland Museum; RMNH, Nationaal Natuurhistorisch Museum, Leiden; UNSW, University of New South Wales, Sydney; UTGD, University of Tasmania Geology Department, Hobart; 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.

Fossils

Elseya (*Pelocomastes*) *lavarackorum* (**Holotype**) Riversleigh, Queensland: registered QM F24121, lodged and registered UNSW AR 1457

Elseya (*Pelocomastes*) sp. inc. ced. – Riversleigh, Queensland: Registered QM F30817, QM F30818, lodged and registered UNSW QMF30817, QMF30818

Elseya (*Pelocomastes*) *uberrima* – Darling Downs, Qld. QMF 9040 (**Lectotype**; Gaffney 1981)

Elseya (*Pelocomastes*) *nadibajagu* – Bluff Downs, Qld.: QMF30576 (**Holotype**), QMF30577

Modern Taxa

Subgenus *Elseya*

Elseya dentata – NHM 1947.3.6.2 (**Paratype**), NHM 1947.3.6.3 (**Paratype**) – Australia. **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 miles S, 3 miles E, Auvergne (Bula) (15°47' S, 130°03' E). **Victoria River** – MV 10406, AM 72947–57, 75070–71, 88442, 93490, NTM 13523, MV 10384–90, 10402–05, 10827–35 Jasper Gorge (16°2' S, 130°41' E); UU 14777 Timber Creek., Timber Creek Store (15°42' S, 130°29' E); MV 10397–99, 10781, 10846, 10850, 10858–60 Timber Creek (15°39' S, 130°29' E); NHM 1947.3.6.3, 1947.3.6.2, 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 72692–94, 72934–46, 73346, 79160 Bullo River at crossing of Katherine – Kununurra Road (15°42' S, 129°38' E); MV 10871–74 Tortoise Reach, Fitzroy Station (15°33' S, 130°52' E). **Daly River** – NTM 32970 18 km north east of Katherine (14°23' S, 132°24' E); NTM 43, NTM 4633 Claravale Crossing, Daly River (14°22' S, 131°33' E); UU 14840–44 Daly R. 2 mile W Claravale Homestead. (14°20' S, 131°33' E). UU 14809 Daly R. (prob. Edith R.14 mile NW Katherine) (14°20' S, 131°33' E); AM 31725 Daly River (14°28' S, 131°41' E); NTM 1220–23, 21152–54 Daly River (13°55' S, 130°56' E); NTM 17201, 17205–06, 17210, UC 0309–19, 0328 Douglas River (13°47' S, 131°17' E); UU 14810–36 Edith Falls, 19.5 miles N, 5 miles W of Katherine (14°12' S, 132°14' E); AM 31728, NTM 13317–21 Edith River (14°28' S, 132°02' E); WA 16516–17, 19906–08, 21594, 24939–40 Katherine (14°30' S, 132°13' E); NTM 3710–13, 3825, NTM 5170, 6583, 32971, AM 45481, 43533 Katherine River (14°28' S, 132°16' E); NTM 13436, 13510 Oolloo Crossing, Daly River (14°04' S, 131°15' E); UU 14837–38 Seventeen Mile Creek 11 mile N 11mile E Katherine (14°18' S, 132°25' E); UU 14839 Ferguson River, 23 miles N, 18 miles W of Katherine (14°04' S, 131°58' E); NTM 32973 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 miles S Darwin) (13°04' S, 130°58' E); NTM 21717 Tjaynara Falls, Litchfield National Park (13°15' S, 130°44' E); UU 14774, 14775 Adelaide Drainage, 60 mile S, 12 mile E Darwin (12°34' S, 131°24' E). **Alligator Rivers Region** – UU 14784–92 Barramundie Creek 3 mile S, 7 mile W Spring Peak (13°01' S, 132°23' E). CRI 2378, Australia: NT: Edith River, CRI 7738, CRI 10909, CRI 10910, CRI 12019, Australia

Elseya flaviventralis (voucher Label *Elseya* sp. aff. *dentata* [Sth Alligator] Georges and Adams 1992, 1996): **Mary River** – UC 0304 Corroboree Billabong, Mary River. **Alligator Rivers Region** – UU 18746–47 Barramundie Creek, 9 km S, 7 km W of Spring Peak (14°49' S, 126°30' E); UU 18740–45 Barramundie Creek, 9 km S, 7 km W, Spring Peak (13°03' S, 132°23'); UU 18748 Barramundie Gorge, 88 km SW Jabiru (13°19' S, 132°26' E); UU 17908–40, AM 129342, UU 18755–56 Bowerbird Lagoon, 15 km S, 16 km E of Jabiru (12°47' S, 133°03'); NTM 34496, NWC 0531, AM 43532 Deaf Adder Creek (13°04' S, 132°58' E); UU 17906–07 Double Billabong, E. Alligator River Arnhem Land (13°09' S, 133°22'); UU 18757–59 East Alligator River Arnhem Land (13°12' S, 133°19' E); UU 18749 Graveside Pool, Jim Jim Drainage (13°16' S, 132°35' E); Jim Jim Drainage, Twin Falls (13°19' S, 132°47') UU 17949–53, 18750–51; AM 128001–04 Magela Creek 12°29' S, 132°52' E); NTM 13985 (**Paratype**) Pul Pul Billabong, South Alligator River (13°34' S, 132°35' E); UU 17904–05 Right Angle Pool, E. Alligator

River (12°53'S, 133°25'); UU 17942–48, 17941 Sandy Billabong 11 km S, 11km E Nourlangie Camp (12°52'S, 132°46'); UU 18752–54 South Alligator R.10 km SE El Sharana (13°34'S, 132°35'E); NTM 13512 (**Holotype**) South Alligator River (13°30'S, 132°28'E); AM 38325–326 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). CRI 4079, Australia: NT: Roper River

Elseya branderhorsti – ANWC R08292, Merauke River, Irian Jaya, Indonesia. PNGM R25201 (**Neotype**), R25202, Bensbach River of the Trans-Fly region of Papua New Guinea (8° 50' 58.6896" S., 141° 14' 52.944" E.), CRI 3657, CRI 4074, CRI 4086, CRI 4087, CRI 4189, CRI 4599, CRI 4913, CRI 4999, Indonesia: Irian Jaya: Merauke, 11922, 13325 Papua New Guinea, 14187, no data

Subgenus *Pelocomastes*

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 QM 48039 Dawson River, Theodore (24°57'S, 150°05'E); QM,28449 (**Paratype**) Emerald, Nogoa 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 west (23°17' S, 150°25'E); UU 17093–95, 17274 Raglan Creek 12.5km W and 1.5km 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 Raglan Creek, near Raglan (23°38'S, 150°49'E); UU 17882–87 Raglan Creek,5.5 km W, 9.3 km S Raglan (23°48'S, 150°46'E). **Burnett River** – QM J81785 (**Holotype**), Ned Churchwood Weir, Burnett River, Qld, Australia, ANWC R6844 Walla Weir, Burnett River (25º 03' S, 152º 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 miles E, 2.8 miles N Gayndah (25°35'S, 151°40'E); QM 48026 Burnett River, Grays Waterhole, near 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, near 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, 1875.5.4.8, 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 0305–06 Mary River (unregistered); QM 36036, 36042, 36045 Tuan State Forest, Tinana Creek, Missings Bridge (25°41'S, 152°53'E); QM 36039, 36041, 36044, 36046–47 Coondoo Creek, Tin Can Bay Road (25°59'S, 152°50'E).

Elseya irwini (voucher label *Elseya* sp. aff. *dentata* [Johnstone] Georges and Adams 1992, 1996): **Cairns district** – AM 68848, 93048 Cairns district (16°55'S, 145°46'E); QM 48062, 48068 Hartley Creek (15°46'S, 145°19'E); AM 125468, QM 23053–54, 23056–57, 23060, 23175–76, 23299–300, 23322, 28954, UU 14871, 14845–70 Malanda, North Johnstone River (17°21'S, 145°35'E); QM 48060 near Cairns (16°55'S, 145°46'E); QM 48059, 48064–65 South Johnstone River (17°38'S, 145°05'E). **Burdekin River** – ANWC 0520 Townsville (19°16'S, 146°49'E); QM 59431 (**Holotype**) Burdekin River (19°42'S, 147°18'E); QM 59021 (**Paratype**) Junction of the Bowen River and Sandlewood Creek, Burdekin Drainage (20°27'S, 147°24'E). **Daintree River** – QM 93362, Douglas creek, Daintree

National Park, Queensland, Australia (–16.28547; 145.27285), QM93360, QM J93361, Daintree River, Daintree National Park, Queensland, Australia (–16.16591; 145.26842), QM J93356–7 Upper Daintree River, Queensland, (16.30601S, 145.15051E); QM J93358–9, Boolbun Creek, Daintree National Park, Queensland, (16.06833S, 145.15454E), CRI 8140, Australia: Queensland: Burdekin River basin

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 miles 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°2'E); UU 14801–08 Gregory River 3.7 miles S, 3.7 miles W Gregory Downs (17°53' S, 139°17'E); QM 31939, 31942, 31944, 31946–47, 31949–50, 31952 Gregory River, Riversleigh 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). **Roper River** – UU 14783 Waterhouse River, 1 mile S, 1 mile E Mataranka Homestead (14°55'S, 133°08'E); AM 13219 Mataranka (14°56'S, 133°04'E).

Subgenus *Hanwarachelys*

Elseya rhodini – PNGM R25203 (**Paratype**), R25204 (**Holotype**), Rue Creek (tributary of Wau Creek), Gulf Province, Papua New Guinea (07°11'67.3" S, 144°37'13.8" E) MCZ134421 MCZ134422 MCZ134423 MCZ134424 MCZ134425 MCZ134426 MCZ134429 MCZ134430 MCZ134431

Elseya schultzei – ZMB 22182 (**Holotype**), near Sae village, Seko coast, near Skosai, ca 5 km W. mouth of Tami River, Papua, Indonesia (2°37'S,140°54'E) ZMB22182 AMNH99613 AMNH99615 AMNH99616 MCZ153907

Elseya novaeguineae – MTKD 8222 (**Holotype**), Passim, Barbussi River, Papua, Indonesia, (1°41'S, 134°05'E), CRI 3133, CRI 6545–49, CRI 6586–88, CRI 6597, Indonesia: Irian Jaya, CRI 3397, captive hatched Germany, CRI 3787 no data ex Calif. Acad. Sci., CRI 4487, 7027, no data.

Myuchelys

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); QM48054–55, no data; UC 2094, South Pine River, Bunya crossing (27°21'S, 152°57'E)

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 – CRI 5391–92, CRI 5449–50, Bellinger River, N.S.W. 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 purvisi – CRI 2196, no data, CRI 2391, CRI 5390, CRI 5393–94, CRI 5447, Manning River, N.S.W., Australia, QM59289–90, Barnard River; AM 123040, 123042, Barnard River Natmap 1: 250000, Hastings SH56–14 488075(31°44'S, 151°51'E)

Supplementary Material 1

Figures S1–S4

Authors: Thomson SA, Friol NR, White A, Wedd D, Georges A (2023)
Data type: .pdf
Explanation notes: Supplementary figures as referred to in the main text.
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Supplementary Material 2

Tables S1–S4

Authors: Thomson SA, Friol NR, White A, Wedd D, Georges A (2023)
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Supplementary Material 3

PAUP output

Authors: Thomson SA, Friol NR, White A, Wedd D, Georges A (2023)
Data type: .pdf
Explanation notes: Output of the PAUP analysis, including the majority consensus and bootstrap consensus trees.
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