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

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**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 once regarded to be *Elseya dentata*. It belongs to a clade including also *Elseya irwini*, *Elseya lavarackorum*, an undescribed form from the Johnstone River of northern Queensland and possibly *Elseya 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 fenestrated head shield and underlying bone, very prominent alveolar and lingual ridges on the triturating surfaces, a serrated margin to the carapace, striking in juveniles and persisting into early adulthood, an anterior plastron that is broad, not oval in outline, and striking 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 south-eastern Queensland.**

**KEY WORDS. – Reptilia; Testudines; Chelidae; *Elseya* sp. nov.; Australian snapping turtle; side-neck turtle, Pleurodire**

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 mccordi* Rhodin (1994b) from the island of Roti in Indonesia, *C. pritchardi* Rhodin (1994a) from New Guinea, *Chelodina burrungandjii* Thomson, Kennett and Georges (2000) from Arnhem Land, *Elusor macrurus* Cann and Legler (1994) from the Mary River in south-eastern Queensland, *Elseya lavarackorum* (White & 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 north-eastern 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 (2000) and *Chelodina alanrixi* de Broin and Molnar (2001). Recent surveys using allozyme electrophoresis (Georges & Adams, 1992, 1996; Georges *et al.*, 2002) have established that many more extant species await description.

The electrophoretic work showed that the genus *Elseya*, in particular, was in need of revision. 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 & 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 is referred to as the *E. dentata* generic group and comprises the type species for the genus *E. dentata*, together with *Elseya branderhorsti*, *Elseya novaeguineae*, *E. shultzii*, *E. irwini* and *E. lavarackorum* (Georges & Adams, 1992;

Thomson *et al.*, 1997). It is anticipated that these two generic groups will one day be recognised as separate genera, thus resolving the paraphyly.

The *E. dentata* generic group, characterised by the presence of an alveolar ridge on the triturating surfaces of the jaw, contains large river turtles distributed from the Mary River of south-eastern Queensland to the Fitzroy River of northern Western Australia. The Australian forms were once regarded as a single species, *Elseya dentata*, but the 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 and name for one of these species, a new form of *Elseya* from the rivers of central coastal Queensland (Fig. 1).

**INSERT FIGURE 1 HERE**

## MATERIALS AND 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 private collection of J.M. Legler (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).

## SYSTEMATICS

*Order:* Testudines Linnaeus, 1758

*Suborder:* Pleurodira Cope, 1864

*Family:* Chelidae Gray, 1831

### *Elseya albagula,* sp. nov.

Southern Snapping Turtle

(Fig. 2, Table 1)

**INSERT FIGURE 2 and TABLE 1 HERE**

*Type Specimens.* – Holotype: ANWC R6844. Adult Female collected by Duncan Limpus on October 24, 2004 from the plunge pool at the downstream side of the Ned Churchwood Weir, Burnett River, Queensland, Australia (25º 03' S, 152º 05' E) (Fig. 2). Allotype: QM 28449 Adult Male from Nogoa River, Fitzroy River Drainage, Queensland, Australia (23º 31' S, 148º 01' E) (Fig. 18). Paratypes: QM 37933 Adult Male from Dawson River Crossing at Baroondah Station, Fitzroy River Drainage, Queensland, Australia (25º 41' S, 149º 13' E); QM 36041 Juvenile from Coondoo Creek, Tin Can Bay Road, Mary River Drainage, Queensland, Australia (25º 59' S, 152º 05' E); QM 36044 Juvenile from Coondoo Creek, Tin Can Bay Road, Mary River Drainage, Queensland, Australia (25º 59' S, 152º 05' E). See Tables 2 and 3 for comparative measurements.

**INSERT TABLES 2 AND 3 HERE**

*Referred Specimens.* – QM 2966, 4501, 4505, 36036, 36039, 36042, 36045-47, 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 *Elseya dentata* generic group, and as such can be distinguished

from all members of the *Elseya 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 *Elseya dentata* generic group by the following combination of characters: Skull robust but acutely narrows across the pterygoids behind the processus pterygoideus externus (Fig. 8); head shield deeply fenestrated to the extent that osteologically there are deep fenestrations in the dorsal surface of the skull also; 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. 8). 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 it obscures the foramen praepalatinum in ventral view.

Anterior carapace blunt, not oval in outline, 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 it begins 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.

*Multivariate Comparisons*. – Species in the *Elseya 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 (Figure 3a): V2/V1 ($R^2$ = 0.70, F=13.52, p<0.0001), IO/HL (partial

**INSERT FIGURE 3 HERE**

$R^2$=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 variate 1 explained 47.8% and canonical variate 2 explained 45.7% of the variation among group centroids. For males, three ratio variables contributed significantly to discrimination among species (Figure 3b): 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. Cross validation error rates in classification to species were 35.1% for females and 14.2% for males. Hence, on the basis of the measurements included in this analysis, discrimination between *Elseya albagula* and the other species is not diagnostic, reflecting the conservatism in overall body form among species in this group.

**INSERT FIGURE 4 HERE**

*Distribution.* – The major drainage basins of the Fitzroy, Burnett and Mary Rivers drainages of south-east Queensland, Australia (Fig. 4), 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 *Elseya albagula* lie with a well defined clade within the *Elseya dentata* subgeneric group comprising *E. irwini*, *E. lavarackorum*,an undescribed form from the Johnstone Rivers region of north coastal Queensland (Georges & Adams, 1996) and possibly *E. branderhorsti* (Thomson, unpub. data), but

excluding *E. dentata*, *E. novaeguineae*, *E. shultzii,* an undescribed form from Arnhem Land and a number of other undescribed species from the New Guinea region.

The closest living relative is regarded to be an undescribed form from the Johnstone Rivers region near Cairns, but among described forms, it is *Elseya lavarackorum* (White & Archer, 1994) (holotype: QM F24121, anterior carapace and plastron from a Pleistocene site at Riversleigh, Nicholson Drainage, Queensland, Australia (18º 35' S, 138º 35' E) not *Elseya irwini* (Cann, 1998) (holotype: QM 59431. Burdekin River, Queensland, Australia, 19º 42' S, 142º 18' E).

## DESCRIPTION

### External Morphology

**INSERT FIGURE 5 HERE**

*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 colour, often also heavily stained. Surface smooth, with or without growth rings, and lacks lustre.

**INSERT FIGURE 6 HERE**

Medial keels distinctive on all major scutes of the carapace of juveniles, forming a tricarinate ridged carapace; absent in adults. Carapace of juveniles serrated from the posterior edge of marginal 1 (Fig. 6); young adults have a serrated margin from marginal 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, moving 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 the sulci. Sulci are straddled by the dark blotches.

*Plastron.* – Plastral formula (using midline length): fem > pec > abd > int > ana $\geq$ hum > gul (Fig. 5). Plastron narrow with axillary width ca 50% of carapace width.

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. Colour of adult plastron often difficult to determine in adults because of complete staining to black, but base colour 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 *Elseya lavarackorum* group; dark brown above, cream, yellow or white below in females; typically grey but occasionally cream below in males. Boundary between light ventral colouration and darker dorsal colouration of head and neck very irregular, forming large, distinctive patches that vary with age and from individual to individual (Fig. 7).

**INSERT FIGURE 7 HERE**

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 fenestrated, involving both scutes and the bone beneath. 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; cream, grey and often suffused with pink; 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 at all bright; the

sclera of the eye is brown; leading and trailing eyespots absent. Upper eyelids 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 colouration and darker dorsal colouration irregular and varies greatly from individual to individual.

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. Four claws on the front feet; five 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 colour of the head and soft parts of juveniles follows that of the carapace. Ventral base colour 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 rictus oris 2/3 of way to shoulder, including 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.). Females grow to a larger size than males (females to 420 mm CL, Mary River M. Dorse, pers. comm.; males to ca 300 mm). Largest examples in this study were a 418 mm female and a 275 mm male (Table 4.). Males easily distinguished from mature females by a much larger tail (Figs 1 & 2), as with all short-necked 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. 8), but to much less a degree than *Elseya dentata*. 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. The alveolar ridge extensive, but not to the extent of *Elseya lavarackorum* (Fig. 8), and begins adjacent to the premaxilla laterally 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 *Elseya lavarackorum*. The lingual ridge is on the premaxilla in the anterior of the skull and continues on to 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 *Elseya lavarackorum* in its widening of the triturating surface. The maxilla and palatines are significantly thickened and the apertura nasalis interna are deeply recessed into the palatal surface of the skull.

**INSERT FIGURE 8 HERE**

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 *Elseya lavarackorum* and *Elseya* sp. aff. *dentata* (Johnstone) – the vomer is expanded posteriorly in *Elseya lavarackorum* and only divides the anterior half of the palatines in *Elseya* sp. aff. *dentata* (Johnstone). Canalis caracoticus internus closed. Foramen anterius canalis caracoti internus absent.

Ventral surface of the skull below the foramen nervi trigemini constricted, to be 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. It extends beyond the occipital condyle, but not to the extent of *Elseya dentata*.

*Cervicals.* – Articulatory formula (Williams, 1950) is the same as for all Chelids turtles and this would appear to be a synapomorphy for the Chelidae, (2(, (3(, (4(, (5), )6), )7(, (8). The atlas axis complex (Hoffstetter & Gasc, 1969) is made up of two neural arches and the first centrum ventrally and an intercentrum anteriorly, these units are sutured to each other as in the primitive condition for many turtle species. Centra of remaining cervicals have well developed sagittal blades which are more prominent at the anterior 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, occupy the middle third of the centrum and protrude horizontally from the neural arch; do not angle downwards as in many other species. Postzygophosis extremely large and almost join in the midline; robust in overall structure. Prezygophosis smaller and extend upwards to meet the postzygophosis of the preceding vertebrae. The neural spine present but small.

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

## 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 substratum. It is typically absent or rare in standing waters impounded

by dams or weirs, unless associated with free-flowing streams. Does not inhabit brackish waters.

*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 eggs are oblong, measuring about 55 mm by 30 mm (Cann, 1998). Eggs in natural nests have been observed to hatch at the end of December. The hatchlings are nearly circular in outline, measuring 51 mm x 50 mm (Cann, 1998). 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*. – *Elseya 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

*Elseya 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. *Elseya dentata* (Gray, 1863) has long been suspected to be a species complex. Both Goode (1967) and Cann (1978) recognised the distinction between populations from the Northern Territory and east coastal Queensland, and anticipated reclassification of the distinctive forms. Legler (1981) recognised five distinguishable allopatric populations of what was then regarded as

*Elseya 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 & 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.*, in prep.). We interpret this sub-structuring 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.

*Elseya albagula* is widespread and locally abundant in three major drainage basins of south-eastern 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 & 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.


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## 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; PW/HW; **24.** PW/HL.

## APPENDIX B

### Specimens Examined

Abbreviations used: AM, Australian Museum; AMNH American Museum of Natural History, New York, USA; 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, the Netherlands; UU, University of Utah collection

of J.M. Legler (UU); 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 QM 48039 Dawson River, Theodore (24 °57' S, 150 °05' E); QM,28449 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 & 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** – 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 (unreg.); 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 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 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, 7mile 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 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).

*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 the 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 18746-47 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 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 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).

*Elseya* sp. aff. *dentata* (Johnstone) (Voucher Label, Georges and Adams, 1992): **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).

*Received*: ###

*Reviewed*: ###

*Revised and Accepted: ###*

## List of Figures

**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 left) is from Barambah Creek, Burnett River and the juvenile (inset right) is from the Mary River, near Kenilworth. Note the prominent serrations on the shell of the juvenile. Photos by John Cann.

**Figure 2.** *Elseya albagula* type specimens: **(a)** the female holotype (ANWC R6844, CL = 382.4) photographed alive; **(b)** the male allotype (QM J28449, CL = 275.5), spirit preserved.

**Figure 3.** Specimens of *Elseya albagula* (●), *Elseya* sp. [Johnstone] (○), *Elseya dentata* (Δ), *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.

**Figure 4.** Distribution of species of *Elseya dentata* subgeneric group in Australia: generalized watershed distributions of *Elseya dentata*, *Elseya lavarackorum* and *Elseya irwini* are shown, with specific localities for *Elseya albagula* (●). An undescribed form (not shown) occurs also in Arnhem Land

**Figure 5.** Dorsal view of the carapace and ventral view of the plastron for (a) *Elseya albagula* (QM59270 CL=377.5 mm); (b) *Elseya lavarackorum* (QM46284 PL= 275.5 mm); (c) *Elseya irwini* (ANWC 0520, CL=281.2 mm) and (d) *Elseya dentata* (QM59277 CL=293.5 mm).

**Figure 6.** Dorsal view of the carapace for small juveniles of (a) *Elseya albagula* (QM36044 CL=91.9 mm); (b) *Elseya lavarackorum* (unreg.); (c) *Elseya* sp. [Johnstone]; (c) *Elseya irwini* (paratype QM59021 CL=103.6 mm) and (e) *Elseya dentata* (AM45481 CL=120.53). Refer also Fig. 1.

**Figure 7.** Lateral view of the head of the holotype of *Elseya albagula*. Note the prominent barbels, prominent tomial sheath, prominent scales on the temporal region and pupil indistinct from iris.

**Figure 8.** Lateral, dorsal and ventral views of the skull of *Elseya albagula* (QM59270 HL=75.7 mm); *Elseya lavarackorum* (QM46284 HL=81.4 mm); *Elseya irwini* (ANWC 0520 HL=69.6 mm); *Elseya dentata* (QM59277 HL=63.8 mm).

## List of Tables

**Table 1.** Measurements of the type specimens. 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).

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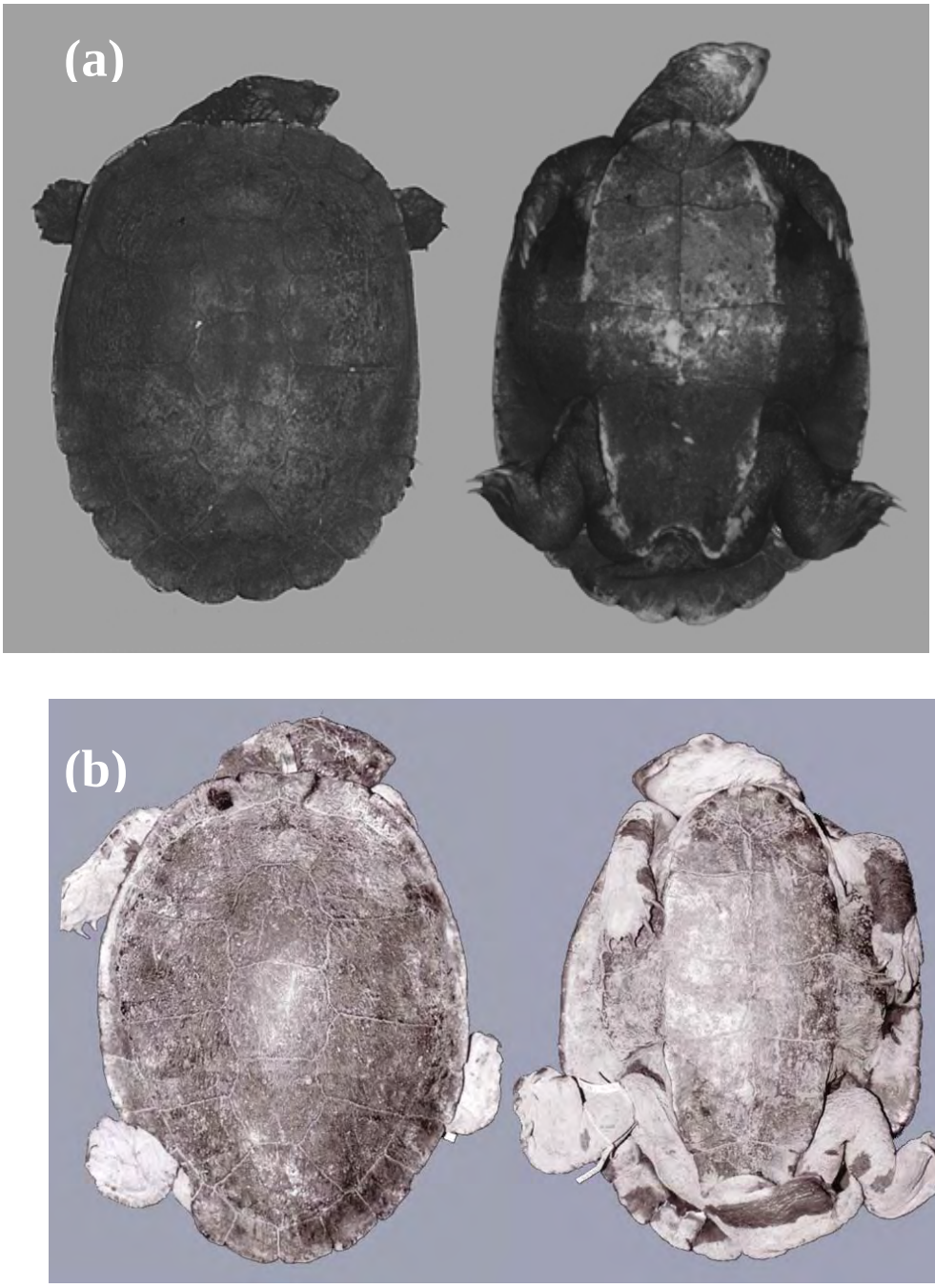


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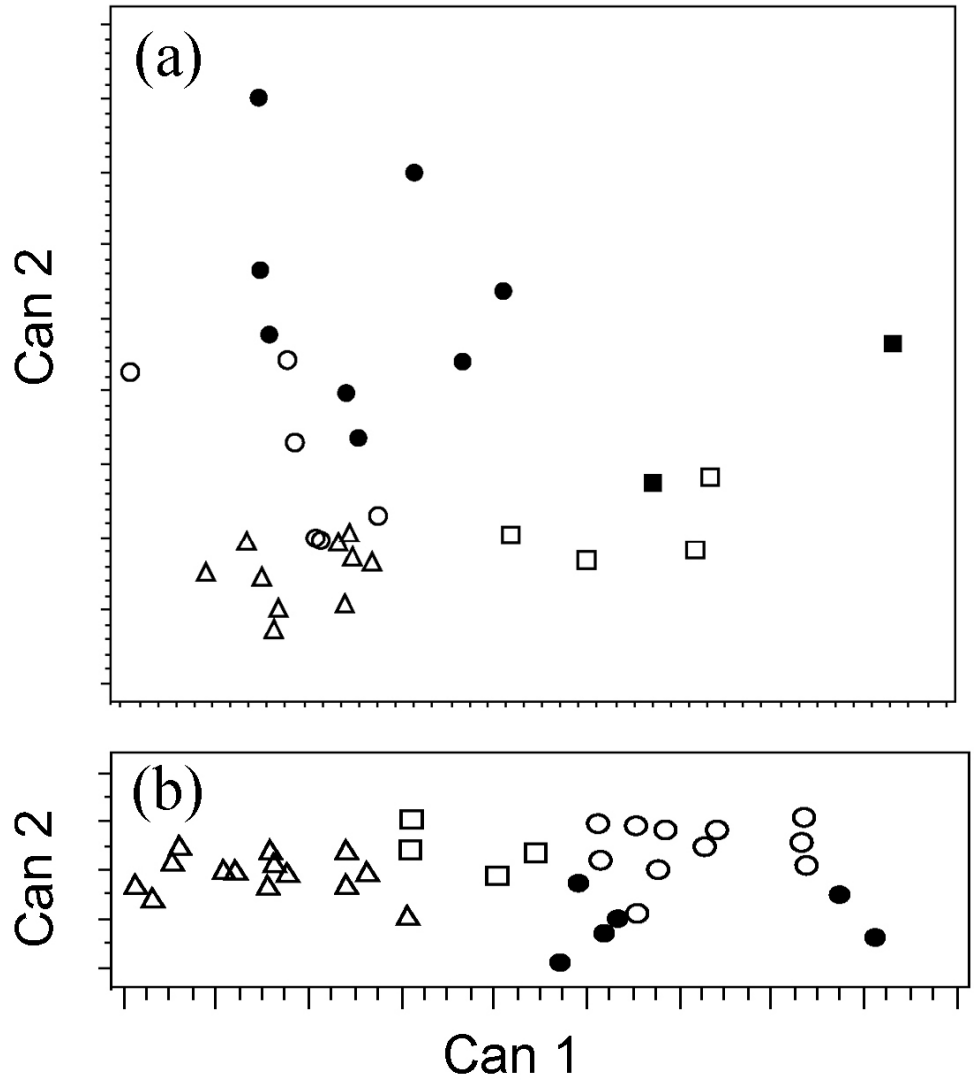


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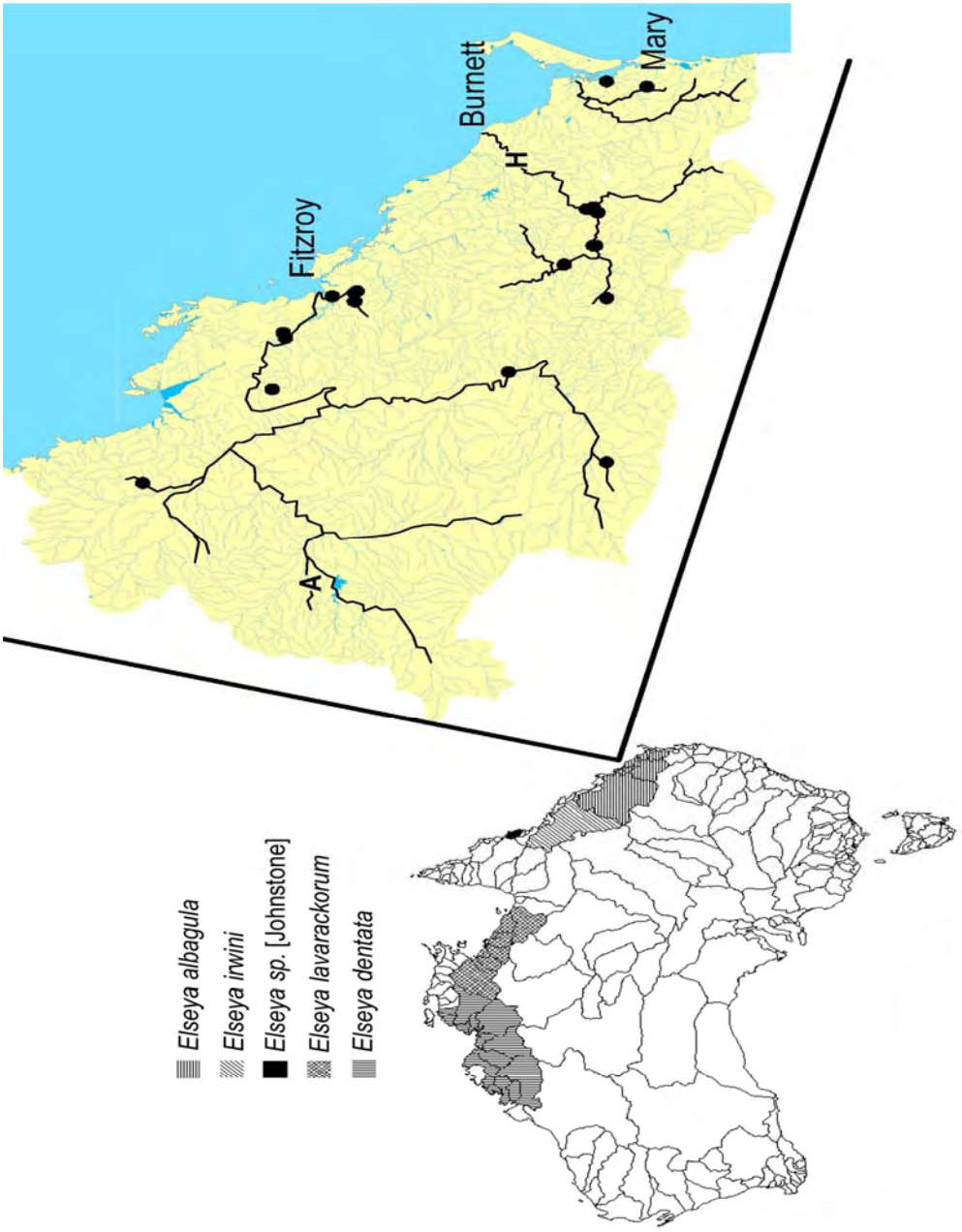


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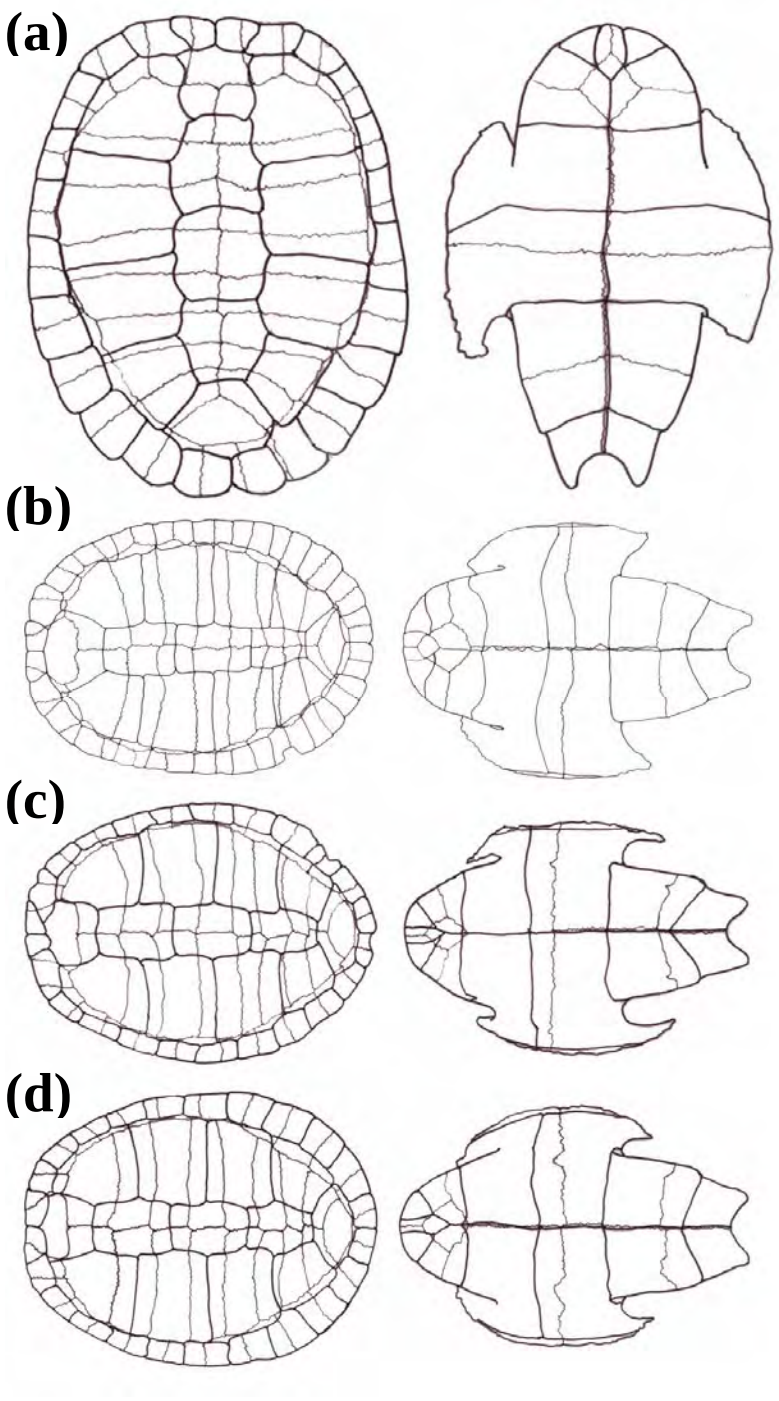


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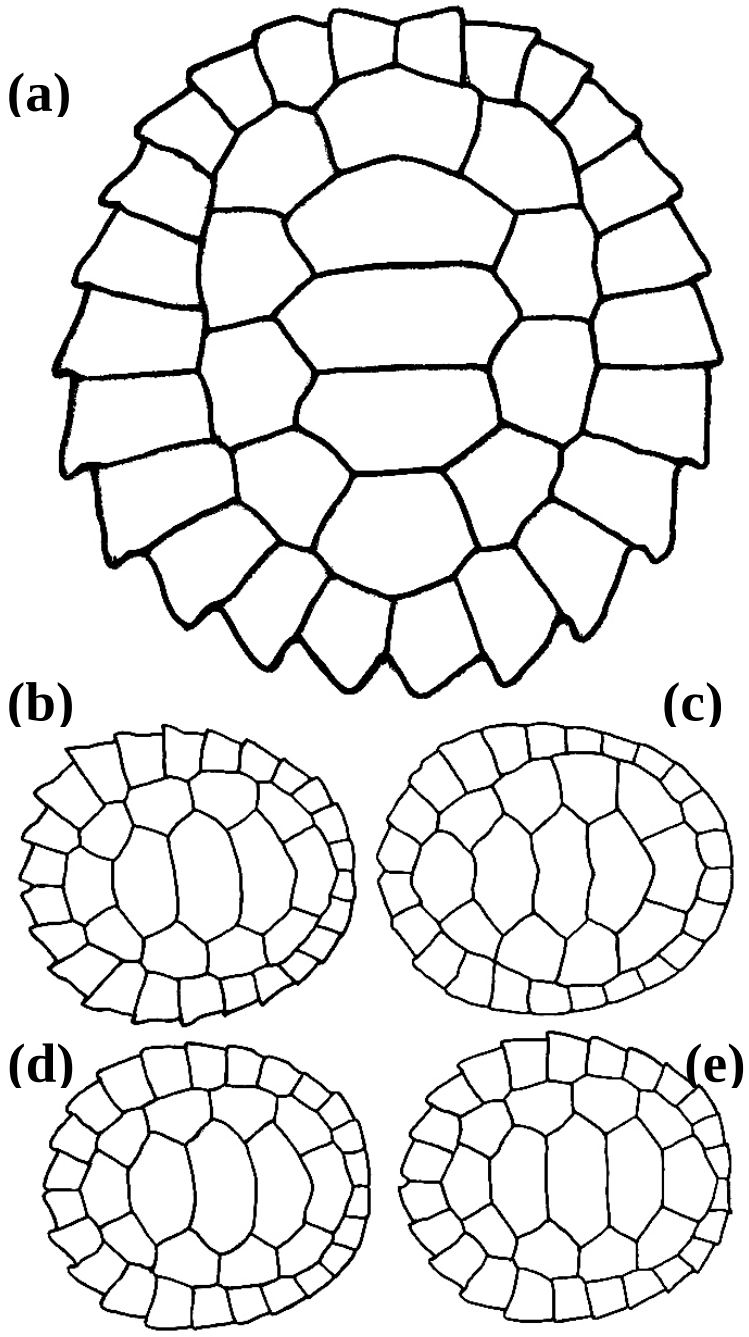


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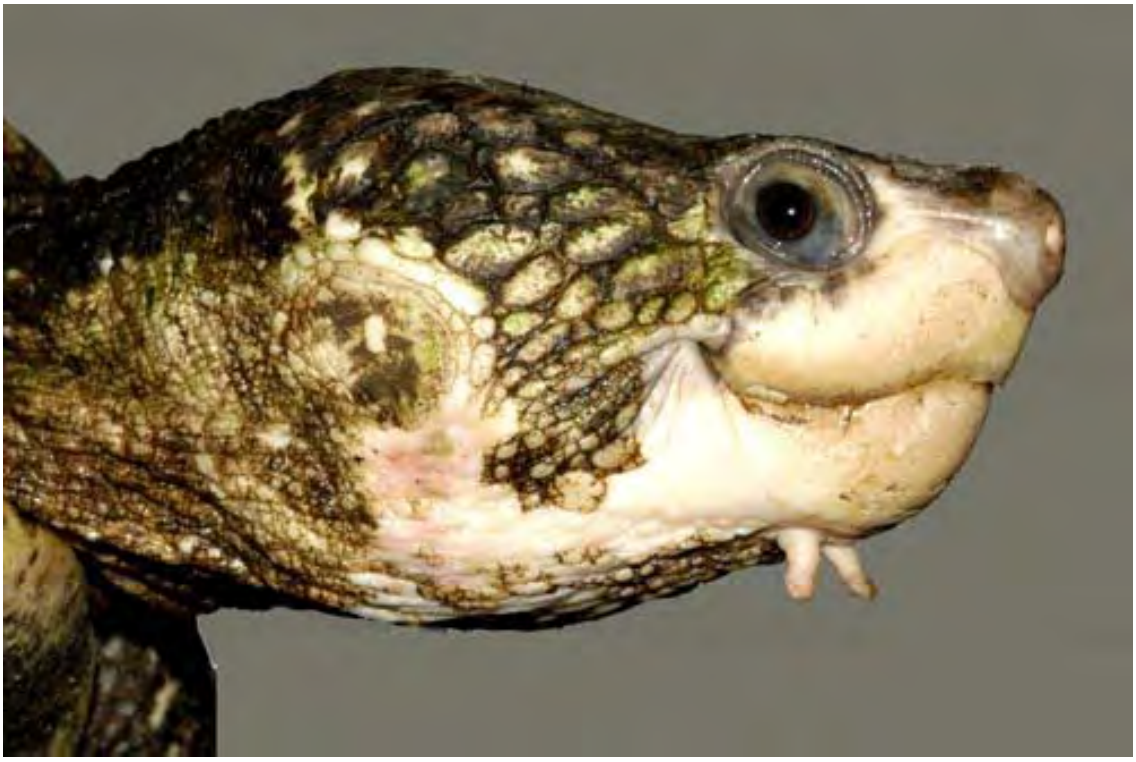

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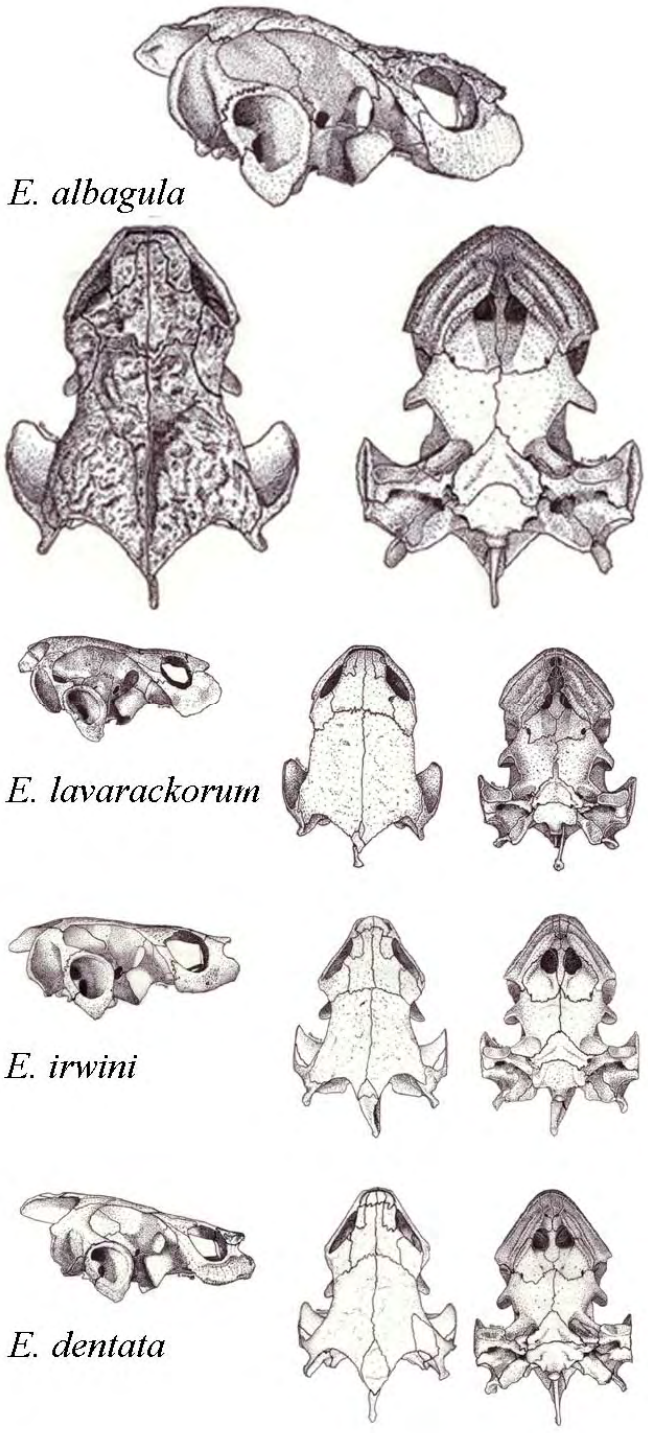


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| MUSEUM # | STATUS | SEX | HL | HW | PW | IO | OD | CL | CW4 | CW8 | V1 | V2 | PL |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANWC R6844 | Holotype | Female | 96.10 | 69.22 | 41.25 | 19.12 | 15.92 | 382.40 | 263.73 | 299.33 | 87.92 | 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 | Juvenile | 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 | Juvenile | 23.54 | 17.6 | 11.65 | 4.01 | 6.62 | 91.89 | 73.02 | 93.88 | 24.32 | 34.36 | 68.34 |

**Table 2.** Relative measurements of the head for *Elseya*. Abbreviations as per Appendix A. Means are given with standard deviations and sample sizes. Non-ratio measurements and ranges in mm.

| SPECIES | SEX | SIZE | HL | HW/HL | PW/HL | IO/HL | OD/HL | HL/CL |
|---|---|---|---|---|---|---|---|---|
| E. albagula | 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) |
| | Male | 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) |
| | | 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) |
| | Female | 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) |
| E. [Johnstone] | Unsexed | 0-200 | 27.5 (1) | -- | 46.9 (1) | 15.8 (1) | 26.7 (1) | 28.8 (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) |
| E. lavarackorum | 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) |
| | Male | 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) |
| E. irwini | 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) | 23.8+0.7 (2) |
| E. dentata | 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) |
| | Male | 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) |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | 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) |
| Female | 200-250 | 50.1 (1) | 70.0 (1) | 42.6 (1) | 19.8 (1) | 19.6 (1) | 25.1 (1) |
| | 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) |

**Table 3.** Relative measurements of the carapace and plastron for *Elseya*. Abbreviations as per Appendix A. Means are given with standard deviations and sample sizes. Non-ratio measurements and ranges in mm.

| SPECIES | SEX | SIZE | CL | HL/CL | CW4/CL | CW8/CL | V1/CL | V2/CL | PL/CL |
|---|---|---|---|---|---|---|---|---|---|
| E. albagula | Unsexed | 0-200 | 149.4+36.5 (9) | 25.7+0.7 (9) | 69.1+5.1 (9) | 87.6+6.6 (9) | 24.7+1.2 (9) | 32.9+2.8 (9) | 76.9+2.0 (9) |
| | Male | 200-250 | 236.6+18.3 (2) | 24.5+1.6 (2) | 71.1+10.6 (2) | 72.1+7.3 (2) | 22.9+0.1 (2) | 23.4+2.8 (2) | 79.8+0.8 (2) |
| | | 250-300 | 267.6+11.5 (5) | 24.0+0.8 (5) | 67.1+1.8 (5) | 78.6+1.4 (5) | 22.3+1.6 (5) | 22.8+2.1 (5) | 81.3+1.8 (5) |
| | Female | 200-250 | 218.2+7.8 (3) | 25.7+0.5 (3) | 68.2+2.8 (3) | 83+1.2 (3) | 24.2+3.6 (3) | 26.0+3.5 (3) | 79.7+0.6 (3) |
| | | 250-300 | 270.5 (1) | 25.9 (1) | 67.6 (1) | 80.7 (1) | 22.3 (1) | 23.1 (1) | 83.7 (1) |
| | | >300 | 387.3+21.7 (4) | 22+0.0 (4) | 67.8+0.0 (4) | 78.6+0.0 (4) | 21.1+0.0 (4) | 19.9+0.0 (4) | 80.7+0.0 (4) |
| E. [Johnstone] | Unsexed | 0-200 | 92.3+4.4 (2) | 28.8 (1) | 69.9+0.4 (2) | 81+3.5 (2) | 26.2+0.4 (2) | 34.4+1.0 (2) | 80.6+0.7 (2) |
| | Male | 200-250 | 215.6+5.1 (8) | 24.5+0.7 (8) | 62.5+2.6 (8) | 74.7+1.3 (8) | 22.8+2.5 (8) | 22.8+1.1 (8) | 79.1+2.4 (7) |
| | | 250-300 | 262.0 (1) | 22.1 (1) | 66.3 (1) | 79.2 (1) | 20.0 (1) | 22.2 (1) | 79.5 (1) |
| | Female | 250-300 | 267.4 (1) | 24.3 (1) | 66.3 (1) | 76.5 (1) | 22.5 (1) | 19.9 (1) | 83.0 (1) |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | >300 | 324.9+30.7 (2) | 24.3+1.4 (2) | 67.5+4.6 (2) | 72.1+0.6 (2) | 23.5+4.0 (2) | 20.4+1.1 (2) | 39.1+55.4 (2) |
| E. lavarack-orum | Unsexed | 0-200 | 154.8+27.8 (7) | 24.0+2.1 (7) | 66.1+1.4 (7) | 82.5+3.8 (7) | 22.7+2.4 (7) | 22.7+2.8 (7) | 78.1+3.0 (7) |
| | Male | 200-250 | 210.3+1.9 (3) | 23.4+0.6 (3) | 64.2+2.4 (3) | 78.6+1.1 (3) | 21.5+2.5 (3) | 19.3+1.3 (3) | 79.4+0.1 (2) |
| | Female | 200-250 | 210.5+13.0 (2) | 24.2+1.4 (2) | 65.8+0.3 (2) | 77.2+2.7 (2) | 24.4+0.0 (2) | 18.8+0.4 (2) | 80.0+1.2 (2) |
| | | 250-300 | 310.9+10.4 (2) | 23.2+0.1 (2) | 62.5+2.1 (2) | 72.3+1.5 (2) | 21.7+1.2 (2) | 16.8+0.5 (2) | 80.2+1.8 (2) |
| E. irwini | Unsexed | 0-200 | 120+23.2 (2) | 27.0+1.1 (2) | 68.1+5.6 (2) | 82.9+8.8 (2) | 29.0+0.4 (2) | 33.4+8.4 (2) | 79.4+2.0 (2) |
| | Female | 250-300 | 335.4+15.7 (2) | 23.8+0.7 (2) | 60.7+2.5 (2) | 71.8+2.9 (2) | 22.5+2.2 (2) | 18.9+0.9 (2) | 78.0+4.4 (2) |
| E. dentata | Unsexed | 0-200 | 159.4+34.7 (9) | 25.4+2.0 (7) | 67.5+5.2 (9) | 83.1+3.4 (9) | 23.1+1.1 (9) | 23+2.8 (9) | 80.9+2.4 (8) |
| | Male | 200-250 | 239.3+12.5 (6) | 24.7+1.2 (6) | 61.7+1.9 (6) | 75.7+2.4 (6) | 20.6+1.7 (6) | 17.2+1.4 (6) | 82.0+1.9 (6) |
| | | 250-300 | 267.3+9.8 (8) | 23.1+1.4 (8) | 59.8+1.6 (8) | 73.4+1.1 (8) | 21.5+0.9 (8) | 16.3+1.1 (8) | 80.9+1.5 (7) |
| | Female | 200-250 | 200.0 (1) | 25.1 (1) | 64.8 (1) | 80.2 (1) | 21.7 (1) | 17.1 (1) | 81.8 (1) |
| | | 250-300 | 279.2+10.6 (10) | 23.6+2.1 (10) | 62.9+2.3 (10) | 74.2+3.4 (10) | 21.6+1.7 (10) | 16.1+0.7 (10) | 83.3+2.0 (9) |
| | | >300 | 314.3+15.9 (2) | 19.7+5.7 (2) | 63.1+0.7 (2) | 74+4.6 (2) | 20.7+1.7 (2) | 15.2+2.2 (2) | 81.8 (1) |