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

Key Words. – Reptilia; Testudines; Chelidae; *Elseya* sp. nov.; turtle; side-neck turtle; taxonomy; systematics; Pleurodira; Australia

The freshwater turtle fauna of the Australasian region is dominated by a single family, Chelidae, found elsewhere only in South America. The taxonomy of Australasian chelids is poorly known, and many species have only recently been described. Those described in the last decade include *Chelodina pritchardi* (Rhodin 1994a) from New Guinea, *C. mccordi* (Rhodin 1994b) from the island of Roti in Indonesia, *C. burrungandjii* (Thomson et al. 2000) from Arnhem Land, *Elusor macrurus* (Cann and Legler 1994) from the Mary River in southeastern Queensland, *Elseya lavarackorum* (White and Archer 1994) first described as a fossil specimen from Riversleigh in Queensland but later established as extant (Thomson et al. 1997), *Elseya irwini* (Cann 1997b) from northeastern Queensland, *Elseya georgesi* (Cann 1997a) from coastal New South Wales and *Emydura tanybaraga* (Cann 1997c) from northern Australia. Several new fossil taxa have been described, including *Elseya nadibajagu* (Thomson and Mackness 1999), *Birlimarr gaffneyi* (Megirian and Murray 1999), *Rheodytes devisi* (Thomson 2000), and *Chelodina alanrixi* (Lapparent de Broin and Molnar 2001).

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

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

METHODS

We examined all available specimens of *Elseya* from the Australian Museum (AM), the Museums and Art Galleries of the Northern Territory (NTM), The Queensland Museum (QM), the Western Australian Museum (WAM), the National Wildlife Collection (ANWC), and the Natural History Museum of London (NHM). Addi-

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

tional specimens in the collection of J.M. Legler at the University of Utah (UU) and the senior author (UC) were also examined as part of the study. Specimens examined are listed in Appendix B. Names of skull elements follows that of Gaffney (1979); shell terminology follows that of Zangerl (1969) with modifications for costals suggested by Pritchard and Trebbau (1984). Bridge strut terminology follows that of Thomson et al. (1997) and Thomson and Mackness (1999).

SYSTEMATICS

Order: Testudines Linnaeus, 1758
Suborder: Pleurodira Cope, 1864
Family: Chelidae Gray, 1831

Elseya albagula, sp. nov.
Southern Snapping Turtle
(Fig. 2, Table 1)

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

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

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

Elseya albagula can be distinguished from species within the *E. dentata* generic group by the following combination of characters: skull robust but narrows acutely across the pterygoids behind the processus

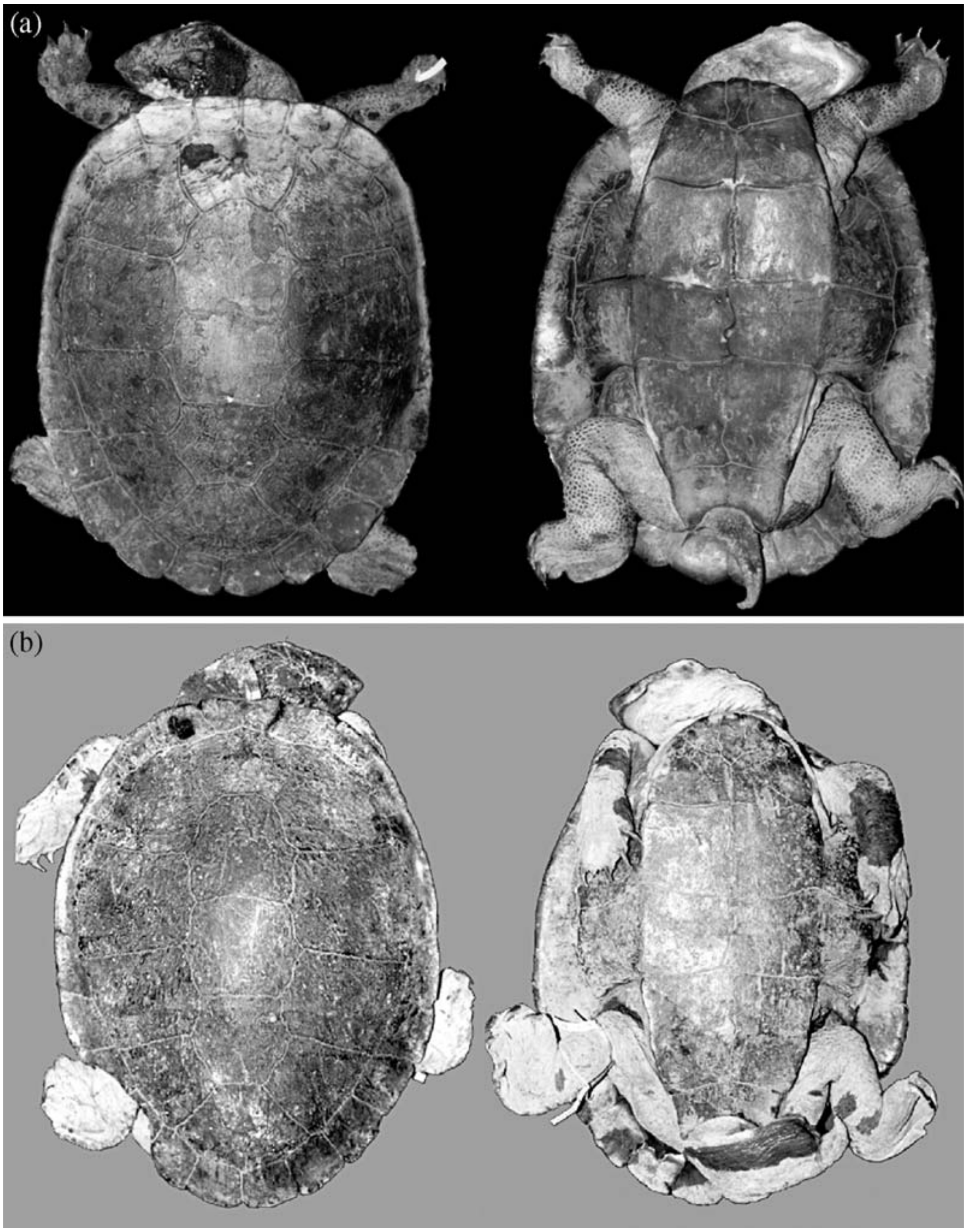

Figure 2. *Elseya albagula* type specimens: (a) the female holotype (Queensland Museum [QM] J81785, carapace length [CL] = 382.4 mm) photographed alive and (b) the male allotype (QM J28449, CL = 275.5 mm), spirit preserved.

pterygoideus externus (Fig. 4); head shield deeply furrowed to the extent that osteologically there are also deep furrows in the dorsal surface of the skull of large adults; alveolar ridge on the triturating surfaces and underlying bone of the upper jaw very prominent, forming a complex with the equally prominent lingual ridge (Fig. 4). This complex corresponds with prominent ridges and cavities in the lower jaw to form shearing surfaces; lingual ridge of maxilla expanded such that, in older specimens, it obscures the foramen praepalatinum in ventral view.

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

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

Table 1. Measurements of the type specimens.[a]

Museum No.	Status	Sex	HL	HW	PW	IO	OD	CL	CW4	CW8	V1	V2	PL
QM J81785	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

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

drainages that comprise its range; also with *Elusor macrurus* in the Mary River and *Rheodytes leukops* in the Fitzroy drainage.

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

Related Taxa. — The affinities of *E. albagula* lie with a well-defined clade within the *E. dentata* subgeneric group comprising *E. irwini*, *E. lavarackorum,* an undescribed taxon from the Johnstone Rivers region of north coastal Queensland (Georges and Adams 1996), and possibly New Guinean *E. branderhorsti* (Thomson, unpub. data, 1996), but excluding *E. dentata*, *E. novaeguineae*, *E. schultzei,* an undescribed taxon from Arnhem Land, and a number of other undescribed species from the New Guinea region.

We consider the closest living relative to be an undescribed taxon from the Johnstone Rivers region near Cairns, but among described taxa, it is *E. lavarackorum* (White and Archer 1994) from the Nicholson Drainage, Queensland, not *E. irwini* (Cann 1998) from the Burdekin River, Queensland.

DESCRIPTION

External Morphology

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

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

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

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

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

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

Boundary between pupil and iris indistinct (Fig. 7), occasionally with a vague lighter ring of gold flecks around the pupil. Iris dull brownish olive, not bright; sclera

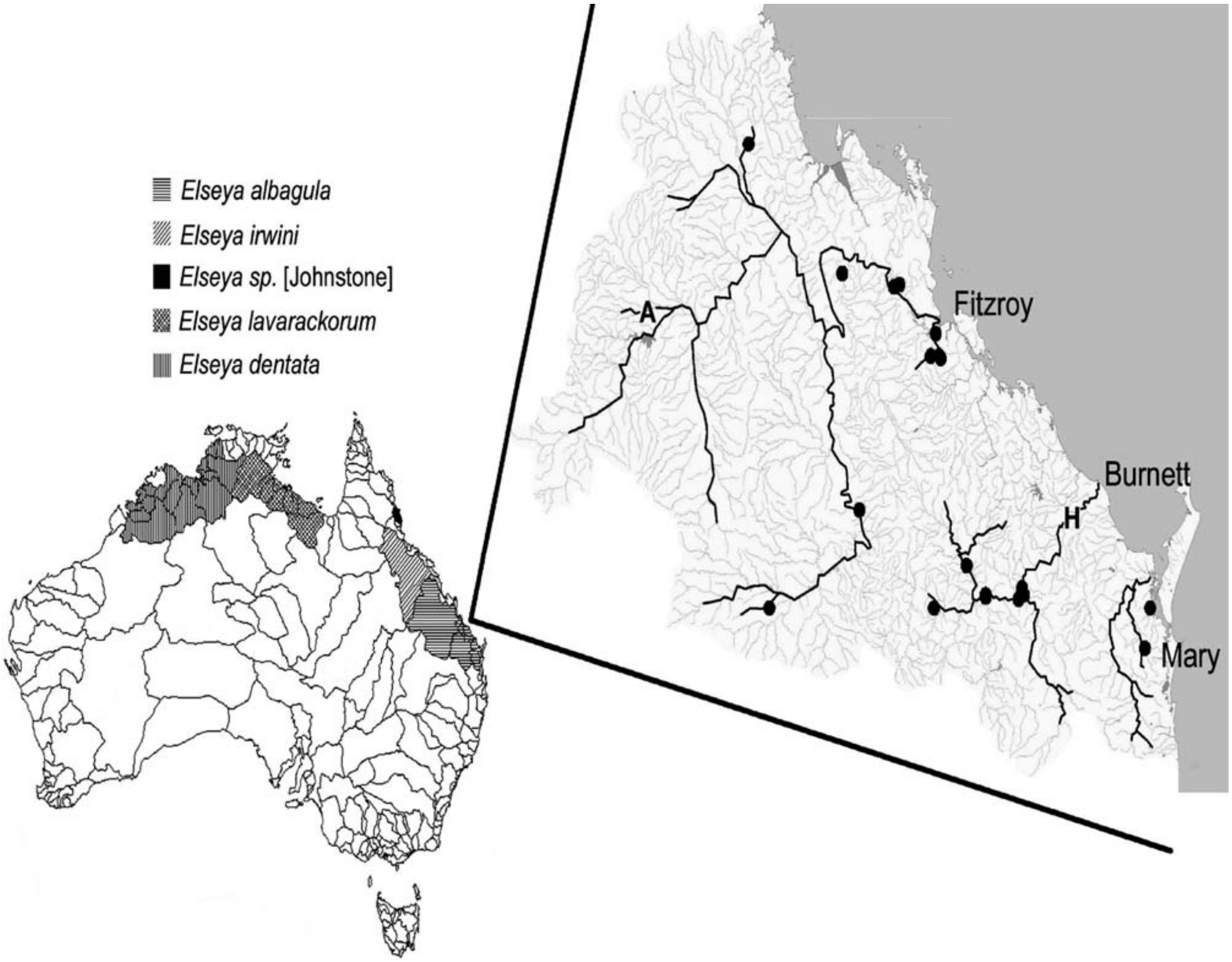

Figure 3. Distribution of species of the *Elseya dentata* subgeneric group in Australia: generalized watershed distributions of *E. dentata (sensu stricto)*, *E. lavarackorum,* and *E. irwini* are shown, with specific localities for *E. albagula* (●). An undescribed form (not shown) occurs also in Arnhem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

brown; leading and trailing eyespots absent. Upper eyelid with nine scales.

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

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

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

Size and Sexual Dimorphism. — This species is among Australia's largest side-necked turtles, with possibly only *Elusor macrurus* attaining a larger size (J. Cann, *pers. comm.*, 1997). Females grow to a larger size than males (females to 420 mm CL, Mary River [M. Dorse, *pers. comm.*, 2004]; males to ca. 300 mm). Largest examples in this study were a 418-mm female and a 275-mm male. Males easily distinguished from mature females by a much larger tail (Figs. 1 and 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. 4, $n = 5$), but to a much

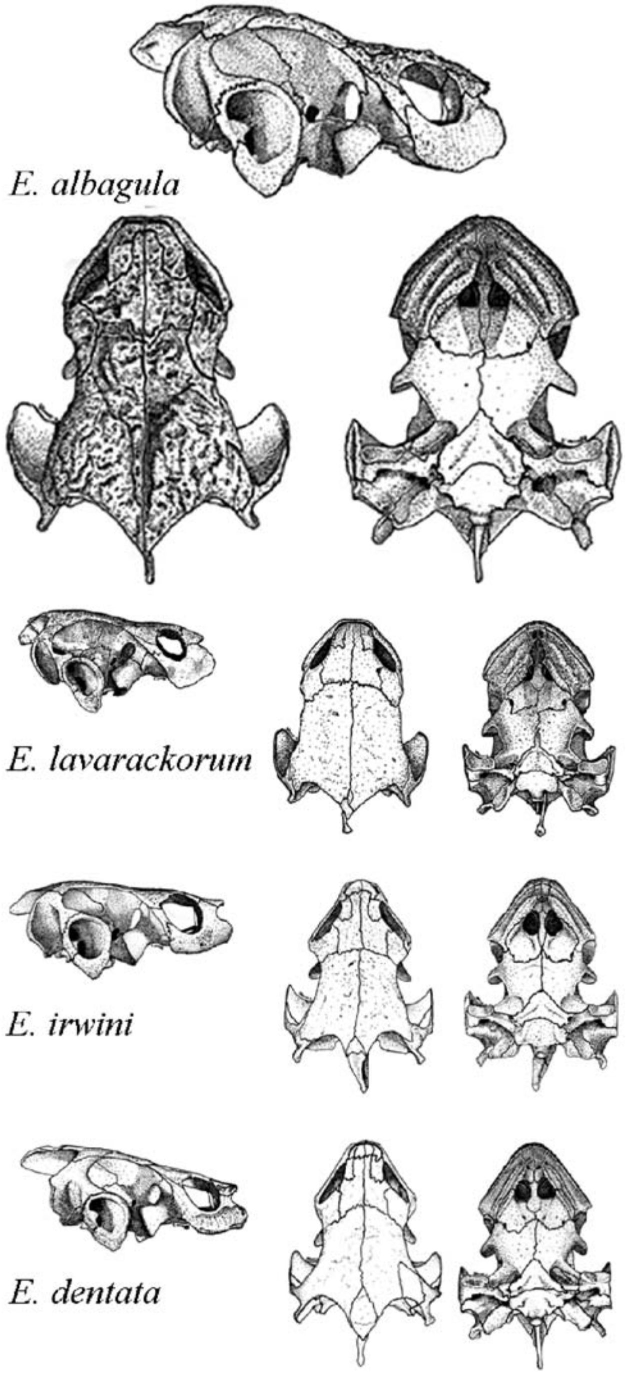

Figure 4. Lateral dorsal and ventral views of the skull of *Elseya albagula* (Queensland Museum [QM] 59270, head length [HL] = 75.7 mm); *Elseya lavarackorum* (QM 46284, HL = 81.4 mm); *Elseya irwini* (National Wildlife Collection 0520, HL = 69.6 mm); *Elseya dentata* (QM 59277, HL = 63.8 mm).

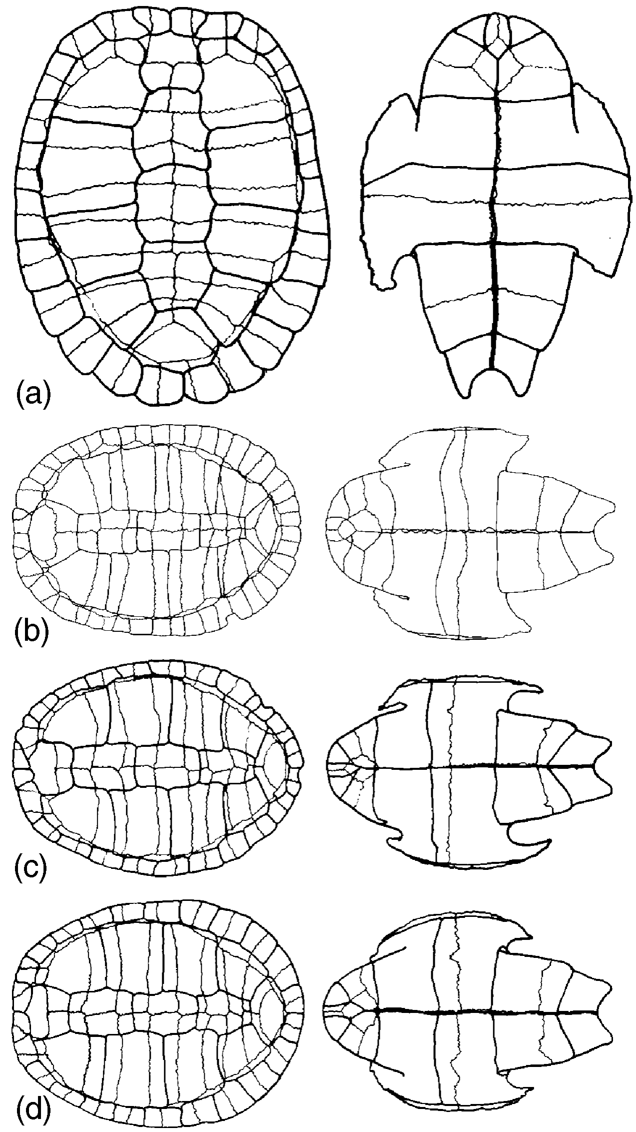

Figure 5. Dorsal view of the carapace and ventral view of the plastron for (a) *Elseya albagula* (Queensland Museum [QM] 59270, carapace length [CL] = 377.5 mm); (b) *Elseya lavarackorum* (QM 46284, plastron length = 275.5 mm); (c) *Elseya irwini* (National Wildlife Collection 0520, CL = 281.2 mm); and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

lesser degree than *E. dentata (sensu stricto)* ($n = 12$). Temporal emargination greater than in any other Queensland *Elseya*; parietal arch wider but not to the extent that it can support the attachment of a head shield. Alveolar ridge extensive, but not to the extent of *E. lavarackorum* (Fig. 8, $n = 2$), beginning adjacent to the premaxilla lateral to the foramen praepalatinum. Alveolar ridge extends back to the end of the triturating surface; does not contact the palatines. Lingual ridge of the triturating surface heavily serrated and widened throughout its length; almost obscures the apertura nasalis interna and completely obscures the foramen praepalatinum from ventral view. The ridge extends back to almost make contact with the pterygoids but does not obscure the anterior edge of the vomer, differentiating it from *E. lavarackorum*. The lingual ridge is on the premaxilla in the anterior skull and continues onto the maxilla but adjacent to the medial edge of the apertura nasalis interna it continues onto the palatine bone. The degree of serrating is moderate but second only to *E. lavarackorum* in its widening of the triturating surface. The maxilla and palatines are significantly thickened and the apertura nasalis internae are deeply recessed into the palatal surface of the skull.

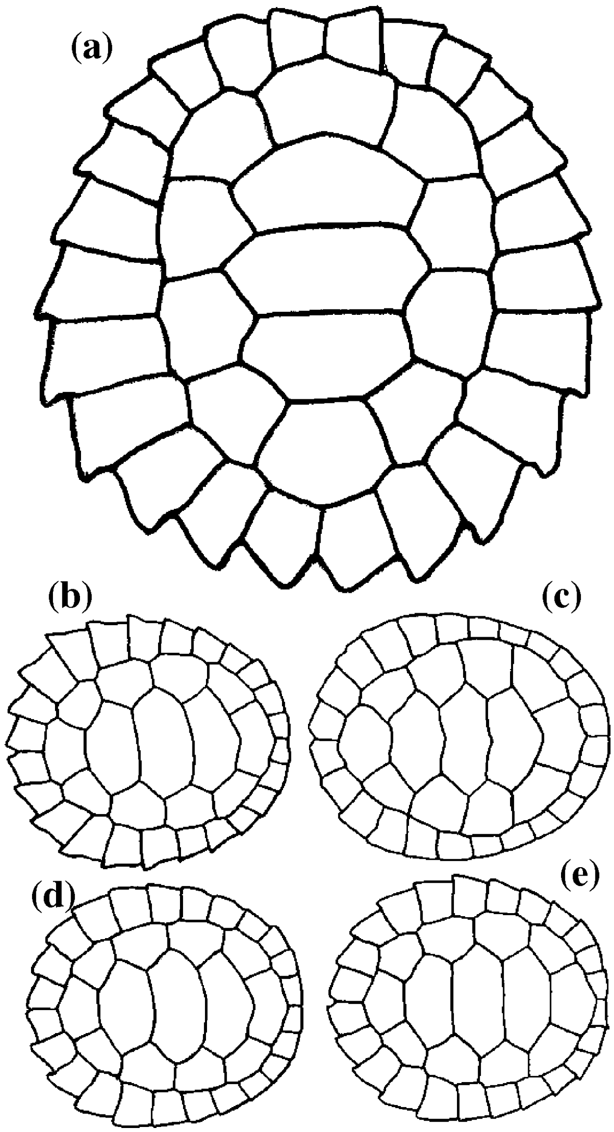

Figure 6. Dorsal view of the carapace for small juveniles of (a) *Elseya albagula* (Queensland Museum [QM] 36044, carapace length [CL] = 91.9 mm); (b) *Elseya lavarackorum* (unreg.); (c) *Elseya* sp. [Johnstone]; (c) *Elseya irwini* (paratype QM 59021, CL = 103.6 mm); and (e) *Elseya dentata* (Australian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

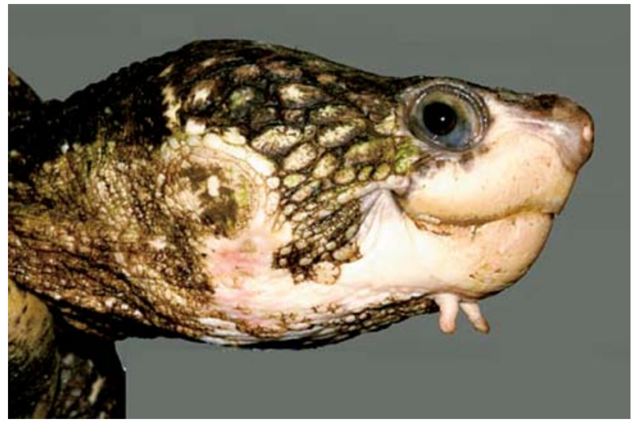

Figure 7. Lateral view of the head of the female holotype of *Elseya albagula* (Queensland Museum J81785, carapace length = 382.4 mm). Note the prominent barbels, prominent tomial sheath, prominent scales on the temporal region, and pupil indistinct from iris.

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

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

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

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

Multivariate Comparisons

Species in the *E. dentata* generic group are conservative in body form, and this is reflected in the outcome of discriminant function analyses. For females, four ratio variables contributed significantly to discrimination among species (Fig. 8a): V2/V1 ($R^2 = 0.70$, $F = 13.52$, $p < 0.0001$), IO/HL (partial $R^2 = 0.44$, $F = 4.34$,

Table 2. Relative measurements of the head for *Elseya*.[a]

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. sp. aff. *dentata* [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)

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

Table 3. Relative measurements of the carapace and plastron for *Elseya*.[a]

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. sp. aff. *dentata* [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. lavarackorum	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)

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

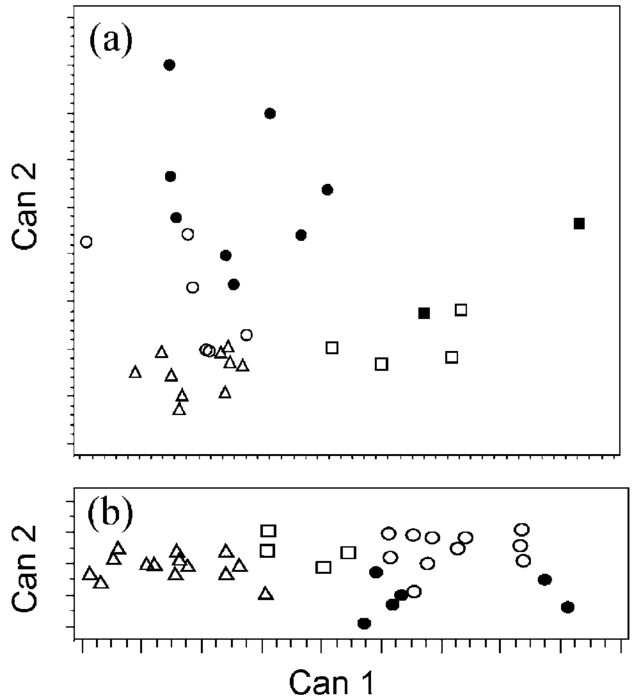

Figure 8. Specimens of *Elseya albagula* (●), *Elseya* sp. [Johnstone] (○), *Elseya dentata* (△), *Elseya lavarackorum* (□) and *Elseya irwini* (■) plotted in canonical variate space: (a) females; (b) males. Axis lengths in proportion to the percentage of variation among species centroids explained by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

$p < 0.01$), 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 (Fig. 8b): V2/CL ($R^2 = 0.82$, $F = 44.96$, $p < 0.0001$), OD/HL (partial $R^2 = 0.40$, $F = 5.99$, $p < 0.005$), and HW/CL (partial $R^2 = 0.30$, $F = 3.78$, $p < 0.05$). Canonical variate 1 explained 80.5%, and canonical variate 2 explained 19.4% of the variation among group centroids. Cross-validation error rates in classification to species were 22.1% for females and 4.1% for males (Table 4). Hence, on the basis of the measurements included in this analysis, discrimination between *E. albagula* and the other species is not diagnostic (Table 4), reflecting the conservatism in overall body form among species in this group.

Ecology

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

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

Diet. — *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) recognized the distinction between populations from the Northern Territory and east coastal Queensland, and anticipated reclassification of the distinctive forms. Legler (1981) recognized five distinguishable allopatric populations of what was then regarded as *E. dentata*: (1) populations in the Ord, Victoria, and Daly systems, and possibly eastward to the Alligator rivers region; (2) populations in the Roper and Nicholson-Leichhardt drainages of the Gulf of

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

	E. dentata	*E. irwini*	*E. lavarackorum*	*E.* sp. aff. *dentata* [Johnstone]	*E. albagula*
E. dentata	**13/11**	–/0	1/2	0/0	0/0
E. irwini	–/0	**–/1**	–/1	–/0	–/0
E. lavarackorum	0/0	–/0	**4/4**	0/0	0/0
E. sp. aff. *dentata* [Johnstone]	0/0	–/0	0/0	**10/4**	1/1
E. albagula	0/1	–/0	0/0	0/1	**6/6**

Carpentaria; (3) the north Johnstone River system of east coastal Queensland; and (4) all populations south of the Atherton tableland, including the Fitzroy River and Burnett River populations. Allozyme studies, using sampling designs based on the extensive field work by Cann, confirmed the existence of a number of genetically distinctive forms, that were sufficiently divergent to be regarded as separate biological species (Georges and Adams 1992, 1996) including with some variation, those identified by the above authors. These new forms are being described progressively (Cann 1997b; Thomson et al. 1997), with this paper contributing to that progress.

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

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

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

Elseya albagula: **Fitzroy-Dawson Drainage**. — UU 17898–903 Connors River 3.5 km W, 3.0 km S, Connors River (22°13′S, 149°01′E); QM 48615 Belmont Creek, Fitzroy River (23°16′S, 150°28′E); QM 37933 Dawson River Crossing, at Baroondah Station (25°41′S, 149°13′E); QM 47987, 47998, 48002, 48010, 48039 Dawson River, Theodore (24°57′S, 150°05′E); QM 28449 Emerald, 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 W (23°17′S, 150°25′E); UU 17093–5, 17274 Raglan Creek 12.5 km W and 1.5 km N Mt. Larcom (23°49′S, 150°52′E); UU 17874–81, 17888–97 Raglan Creek 3.7 km E, 8.5 km S Raglan (23°48′S, 150°51′E); AM 129338–40, QM 59269 Raglan Creek, nr. Raglan (23°38′S, 150°49′E); UU 17882–7 Raglan Creek, 5.5 km W, 9.3 km S Raglan (23°48′S, 150°46′E). **Burnett River** – QM J81785, 59270 Walla Weir, Burnett River (25°03′S, 152°05′E); UU 17086–92 Barambah Creek 7.8 km S, 9.2 km E Gayndah (25°41′S, 150°48′E); UU 14872 Barambah Creek 3.2 mi E, 2.8 mi N Gayndah (25°35′S, 151°40′E); QM 48026 Burnett River, Grays Waterhole, nr. Gayndah (25°37′S, 151°37′E); QM 48029, 48052 Burnett River, Jones Weir (25°36′S, 151°18′E); QM 48027 Burnett River, Mundubberra (25°35′S, 151°18′E); QM 48012, 48046 Burnett River, nr. Gayndah (25°37′S, 151°37′E); QM 2966, AM 6110, Eidsvold (25°22′S, 151°07′E); NHM 75.5.4.8, 76.5.19.77, 1875.5.4.7–8, QM 4501, 4505 Gayndah

(25°37′S, 151°37′E); AM 123067 Grey's Waterhole, Burnett River (25°32′S, 151°39′E). **Mary River** – UC 0305–6 Mary River; QM 36036, 36042, 36045 Tuan State Forest, Tinana Creek, Missings Bridge (25°41′S, 152°53′E); QM 36039, 36041, 36044, 36046–7, 59271 Coondoo Creek, Tin Can Bay Road (25°59′S, 152°50′E).

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

Elseya lavarackorum: **Roper River**. — NTM 16328–30 Red Lilly Lagoon, Roper River (14°42′S, 134°05′E); UU 14779–82 Roper River 1.5 mi W Elsey Homestead (14°59′S, 133°19′E); UU 14778 Roper River Elsey Homestead (14°58′S, 133°20′E). **Gregory-Nicholson Drainage** – QM 47908, 47911, 48547, 48564 Elizabeth Gorge, Bowthorn Station (18°13′S, 138°2′E); UU 14801–8 Gregory River 3.7 mi S, 3.7 mi W Gregory Downs (17°53′S, 139°17′E); QM 31939, 31942, 31944, 31946–7, 31949–50, 31952 Gregory River, Riversleigh Station, N of Mt Isa (19°02′S, 138°45′E); UC 0201, QM 48544 Lawn Hill Gorge (18°46′S, 138°25′E); QM 46284 Lawn Hill National Park (18°35′S, 138°35′E). **Roper River** – UU 14783 Waterhouse River, 1 mi S, 1 mi E Mataranka Homestead (14°55′S, 133°08′E); AM 13219 Mataranka (14°56′S, 133°04′E).

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

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

Elseya sp. aff. *dentata* (Johnstone) (Voucher Label, Georges and Adams, 1992): **Cairns District**. — AM 68848, 93048 Cairns district (16°55′S, 145°46′E); QM 48062, 48068 Hartley Creek (15°46′S, 145°19′E); AM 125468, QM 23053–4, 23056–7, 23060, 23175–6, 23299–300, 23322, 28954, UU 14845–71 Malanda, North Johnstone River (17°21′S, 145°35′E); QM 48060 nr. Cairns (16°55′S, 145°46′E); QM 48059, 48064–5 South Johnstone River (17°38′S, 145°05′E).

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