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The Mary River Tortoise: A New Genus and Species of Short-Necked Chelid from Queensland, Australia (Testudines: Pleurodira)

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ABSTRACT. – **A new genus and species of short-necked turtle of the family Chelidae is named and described from the Mary River of extreme southeastern Queensland, Australia (just north of Brisbane). For approximately 25 years the taxon has been known only from specimens purchased in pet shops. This turtle is probably the largest Australian shortneck and is diagnosed by a suite of characters, including a tail structure that is unique among chelids. The tail is laterally compressed and the distal caudal vertebrae bear haemal arches. The tail of adult males is larger than in any known chelid – up to 70% of carapace length. Relationships to other chelids are not completely clear. Multidiscriminate analysis of 6 generic groups of shortnecks suggests membership of the new taxon in a group including *Elseya dentata*, *Elseya latisternum*, and *Rheodytes*. A preliminary cladistic analysis suggests the new taxon to be the sister group of *Rheodytes* and for both of these genera to be most closely related to *Elseya dentata*, with *Elseya latisternum* more distantly related to all three genera.**

Pet shops in Adelaide, Brisbane, Melbourne, and Sydney began receiving large numbers of unusual hatchling turtles in approximately 1961. These turtles were referred to as "saw-shelled snappers" (*Elseya latisternum*) but they were distinct from any known Australian chelid. The specimens sold were uniform in size (ca. 36 mm carapace length, 7 g), active, in good health, and were probably stocked within a few weeks of hatching. Annual shipments continued until approximately 1974 when it became illegal to sell turtles in Victoria. Sales continued sporadically thereafter.

Most of the turtles sold probably died. Most museum collections in Australia have at least a few small juveniles which were obviously in bad condition prior to preservation. Some that survived and grew were released in urban reservoirs or donated to zoos. A few remain in private collections.

We have jointly gathered information on this taxon since 1974. For working purposes we coined the epithet "Shortneck alpha". There have been a few references to this taxon in the literature (Cann, 1981; Georges and Adams, 1992; Legler, 1993a), but none in a taxonomic context. By 1988 the existence of "Shortneck alpha" was common knowledge in the Australian herpetological community.

From 1980 to 1988 we explored natural drainage systems ranging from the upper Murray-Darling system to the Kimberley region without finding the natural provenance of this animal. It was impossible to obtain useful information from pet dealers or distributors. Some of the specimens we examined prior to 1990 may have been caught in the wild, but no localities were available.

In October 1990 Cann obtained four adult specimens in the Mary River of Queensland. Thus, at length, we are describing this new taxon known heretofore only from captive specimens, pet shops, and urban reservoirs.

METHODS AND MATERIALS

Specimens Examined. — This description is based on 41 specimens of the new taxon, of which only the types have precise locality data. Comparative materials consist of the following specimens (most of which are currently stored at the University of Utah): *Elseya* (*dentata*) group, 405; *Elseya* (*latisternum*) group, 865; *Rheodytes*, 73; *Emydura*, ca. 1000.

The type specimens were obtained by diving in murky water. The many juveniles sent to pet shops were hatched from artificially incubated eggs after being transplanted from fresh natural nests.

Maps. — All localities mentioned can be found on the following maps: Australia 1:250,000, SG 56-6, Maryborough, Ed. 1, Series R502; Operational Navigation Chart, 1:1,000,000, Sheet Q-15, Ed. 4; Reader's Digest Atlas of Australia, 1:1,000,000, Map 14 Maryborough, Map 15 Brisbane.

Terminology. — The terminology used for turtle structures is that of Carr (1952), as used by Legler and Cann (1980) and Legler (1993a, 1993b) (see Figs. 1 and 7). Abbreviations of plastral scutes are: G, gular; IG, intergular; Hum, humeral; Pec, pectoral; Ab, abdominal; Fem, femoral; An, anal. A plastral formula consists of the plastral scutes listed in order of midline length; e.g., a formula of "653412" (An>Fem>Pec>Ab>IG>Hum) for the plastral scutes indicates that the anal is longest, the femoral next longest, etc. Plastral formulae were calculated with a Fortran program which ranked ties in descending order (e.g., if scutes 1, 3, and 2 were of equal length, they would be expressed as "321" (Pec≈Hum≈IG) in the formula.

Abbreviations used for museum specimens are as follows: AMR, Australian Museum, Sydney; QMJ, Queensland

Museum, Brisbane; NMV, National Museum of Victoria, Melbourne; UU, University of Utah, Salt Lake City.

Legler's work on the genera of Australian chelids is not yet complete. Generic groups within *Chelodina* and the two within *Elseya* are referred to provisionally as *Chelodina* (*expansa*), *Chelodina* (*longicollis*), *Elseya* (*dentata*) and *Elseya* (*latisternum*), respectively. All numeric data for the present analysis reside in ASCII files at the University of Utah.

Statistics and Analysis. — Stepwise discriminant analysis was done with BMDP7M (Dixon, 1988) on a Microvax minicomputer. Forty characters were used as follows. Measurements of shell (9) – length of carapace, width of carapace, height of shell, length of bridge (mean of two sides), length of plastron (maximal), four separate widths of plastron (humeropectoral, axillary, inguinal, midfemoral); head (4) – width of head (maximal), least interorbital breadth, greatest diameter of orbit, length of mandibular symphysis; plastral scutes (8) – length and width of intergular, interlaminal lengths of gulars, humerals, pectorals, abdominals, femorals, and anals; carapacial scutes (11) – lengths of centrals [vertebrals] 1-5, anterior and posterior widths of C1, widths of C2-C5. Quantified character states (8) – precentral [nuchal] scute (+ or -), number of barbels, supernumerary scutes (+ or -), and the alignment of the five interlateral seams in relation to the marginal scutes. Figure 1 explains the quantification of seam alignments (modified from Tinkle, 1962) and any shell measurements which are not self-explanatory.

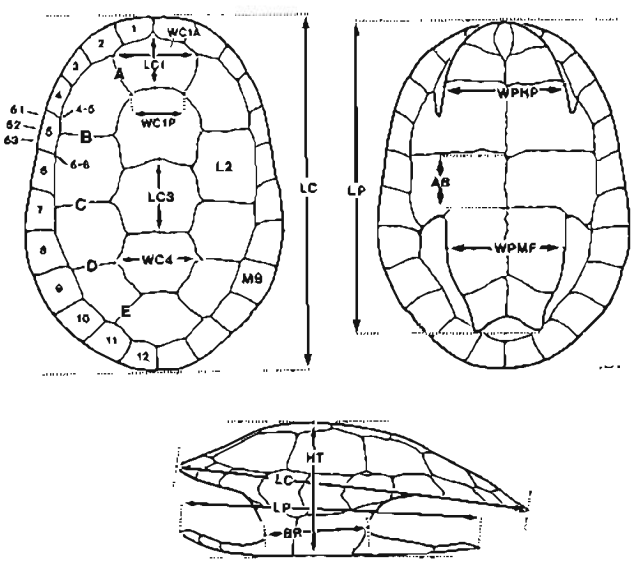

Figure 1. Dorsal, ventral, and lateral views of an *Emydura* shell showing methods of measuring chelid turtles and expressing interlaminal seam contacts. Abbreviations: AB, abdominal scute; BR, length of bridge (minimal); HT, height of shell; L2, second lateral scute; LC, length of carapace (maximal); LC1-5, lengths of central scutes; LP, length of plastron (maximal); M9, ninth marginal scute; WC1A and WC1P, anterior and posterior widths of C1; WC2-5, widths of central scutes; WPHP, width of plastron, humeropectoral; WPMF, width of plastron, midfemoral. Length of plastron and carapace are maximal and include any notches or depressions. Method of measuring plastral scutes of unequal length yields a single measurement which is a mean. Dotted lines show orientation of caliper jaws. The main measurements of the shell approximate the smallest rectilinear box into which the shell would fit. Other measurements used but not illustrated are: WC, width of carapace (maximal); WH, width of head (tympanic); and WT, weight. Interlateral-marginal seam contacts on this specimen would be expressed as follows: A2, B5 (B51 if contacting anterior portion of M5, B52 if middle portion, B53 if posterior portion), C7, D9, E11 (E113 would mean contact with posterior portion of marginal E11).

All measurements were transformed as percentages of carapace length. Carapace length itself was used in the analysis of adults but not of immature stages.

BMDP7M expresses the discriminative value of each character used. Each individual is plotted on a scattergraph according to its *a priori* assignment to a population. BMDP7M expresses the accuracy of these assignments in terms of percentage of specimens "correctly" assigned for each population. The program generates canonical axes equal to the number of populations plus one but plots only the first two axes (= canonical "variables" = the X and Y axes, respectively). JMP (SAS Institute Inc., Lehman et al., 1989) is a microcomputer statistical program which permits the three dimensional plotting of the X, Y, and Z axes generated in BMDP7M. JMP permits rotations of the plot in three dimensions to optimize the viewing of the population clusters and centroids. The results of the analysis (i.e., the interrelationships of populations) were essentially the same whether the logs of ratios or the ratios themselves were used.

A preliminary cladistic analysis of 8 hypothesized Australian genera was based initially on 82 characters; these included the 19 allozymes used in the analysis of Georges and Adams (1992) and 63 characters from an extensive comparative table being prepared by Legler. Minimal trees were generated in PAUP 3.0 (Swofford, 1990) (exhaustive search, with *Chelodina* as the outgroup, characters unordered and of equal weight). The long-necked genera *Chelodina* (*expansa*) and *Chelodina* (*longicollis*) were then excluded and the characters culled to a total of 51 by omitting redundant, invariate, or questionable characters. The final database consisted of: 8 skull characters, 5 shell shape and structure, 2 tail, 1 diet, 3 reproduction, 1 adult size, 4 scutes, 7 skin, 2 viscera, 2 karyotype, 16 allozymes (see Table 4). The analysis was then repeated in PAUP with virtually identical results. Trees generated in PAUP were studied in MacClade (Maddison and Maddison, 1992).

"Sternal index" (see Table 4) is useful in quantifying general shell shape and estimating volume of the sternal cavity. It is based on the formula: length of bridge x width of carapace x height of shell / 1000 = rectilinear estimate of sternal capacity in cc. See Legler (1993a) for comparison of shell shapes.

SYSTEMATICS

This taxon is allied to and shares characters with all the non-*Pseudemydura* short-necked genera but it is distinguished from these taxa and from all other chelids by a unique, laterally compressed tail containing haemal arches. We therefore deem it appropriate to place the taxon in a new monotypic genus.

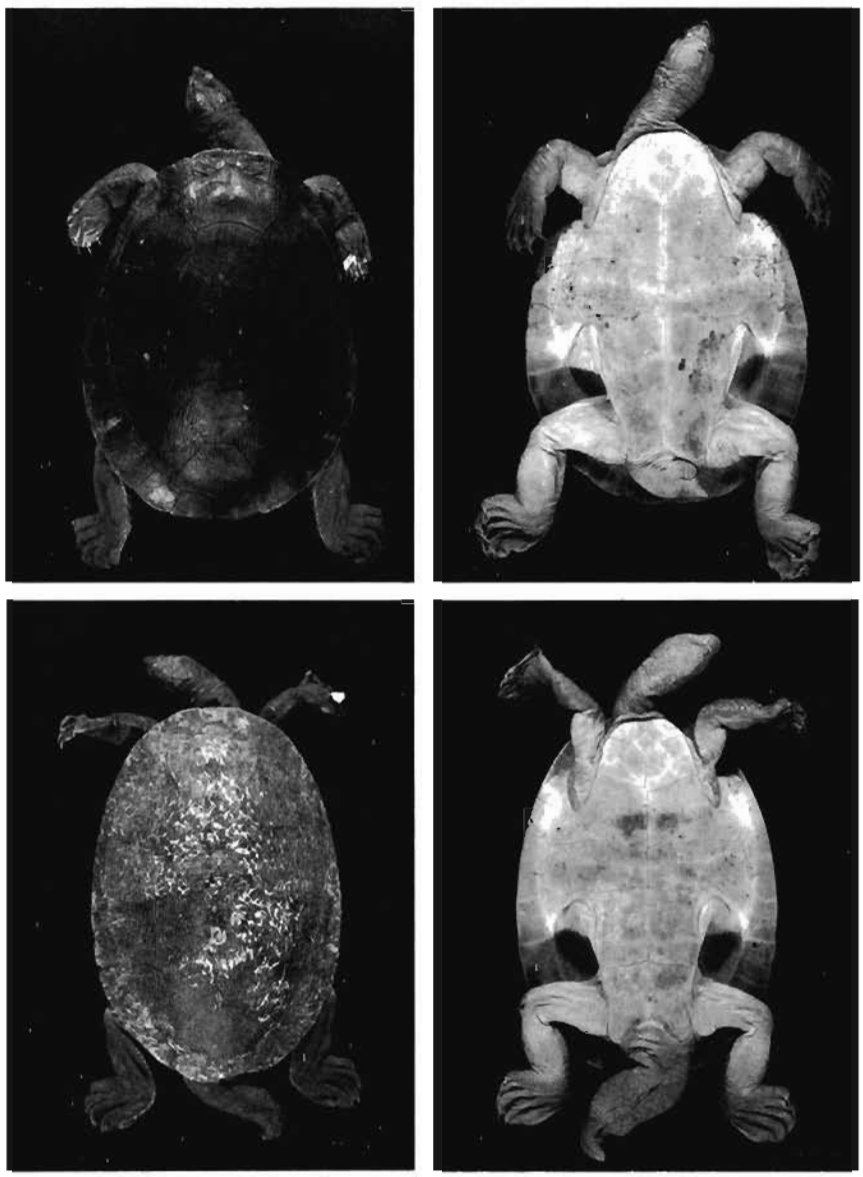

Figure 2. Dorsal and ventral views of the female holotype, QMJ 51275 (upper) and the male allotype, QMJ 51274 (lower) of *Elusor macrurus*. Carapace lengths 312 mm and 347 mm, respectively.

***Elusor*, Gen. nov.**

Type Species. — *Elusor macrurus*, sp. nov., by monotypy.

Vernacular Name. — Mary River Tortoise.

Etymology. — *Elusor*: L. *eludo*, to escape, to escape notice of; ergo, a contrived word of male gender connoting a frustratingly elusive thing, alluding to the cryptic provenance of this organism during the many years we knew it existed; *macrurus*: Gr. *makros*, long, + Gr. *oura*, tail; referring to the long and distinctively shaped tail.

Diagnosis of Genus. — A short-necked Australian chelid turtle of large adult size, with a low streamlined shell, basking habits, and a southern temperate breeding pattern. Distinguished from all other Australian chelid turtles by the following combination of characters (characters marked with an asterisk [*] are alone diagnostic): 1. Eye dull and dark with a vestigial nictitating membrane*. 2. Barbels long and fleshy. 3. Humerus and femur of subequal length*. 4. Inguinal and axillary buttresses of subequal size*. 5. Precentral [nuchal] scute always present. 6. Tail distinctive (all sexes and ages) in having a large precloacal portion*, a longitudinal, slitlike cloacal orifice*, and in being laterally compressed*. 7. Distal caudal vertebrae much higher than long and bearing distinct haemal arches*. 8. Length of tail in adult males more than half length of carapace and significantly longer than combined length of head and neck*.

***Elusor macrurus*, sp. nov.**
(Figures 2-8, Table 1)

Holotype. — QMJ 51275, whole, preserved adult fe-

male with carapace length of 312 mm, collected 16 October 1990 by John Cann; Mary River, 45.5 km S and 21.0 km W Maryborough, Queensland, Australia, elevation approximately 30 m (25°58'S, 152°30'E). Specimen bears a small, rectangular fiber tag on right forefoot ("QD MUS J51275") and the left anterior edge of the carapace has incurred a small crack since preservation.

Allotype. — QMJ 51274, whole, preserved adult male with carapace length of 347 mm, same data as holotype, tag on right forefoot ("QD MUS J51274"), a small chip on the right posterior edge of the carapace.

Paratypes. — AMR 138841, juvenile, hatched from egg laid by holotype; QMJ 51468-70, 54138-40, AMR 138839-40,138842, juveniles hatched from eggs taken from several nests; AMR 134981, female, 326 mm, partially dissected and partially skeletonized; AMR 134982, male, 378 mm, live at this writing; Mary River, 23.5 km S and 17.5 km W Maryborough, Qld., elevation approximately 25 m (25°45'S, 152°32'E).

Other Specimens. — The following museum specimens of unknown origin are referred to this taxon: UU 18004-06, 19487, juveniles; UU 18007, 19484, 19501, immature subadults; UU 19508, partial subadult skeleton; UU 19486, male; AMR 125482-85, 128006, juveniles; AMR 140845, partial adult male skeleton; NMV D-65881, immature skeleton; NMV D-65882-3, 65885-92, immature subadults; NMV D-65884, immature female.

Diagnosis. — As for genus *Elusor*.

GENERAL DESCRIPTION

External Morphology

Shell. — General appearance of adults massive, smooth, streamlined, dull and unpatterned; males depressed; females variable in cross section. Shape in dorsal aspect variable; holotype wider posteriorly than anteriorly, female paratype definitely tapered posteriorly, allotype narrow and nearly straight-sided (Fig. 2). Depth sexually dimorphic. Optical cross-section of adults evenly rounded from edge to edge; no dorsal flaring of marginals; a slight middorsal depression; never a middorsal keel, ridge, or prominence in adults. Plane from marginal edge to edge of plastron straight or convex. Optical cross-section of immature animals significantly different from adults: marginals flared dorsally; an angled juncture of plastron and bridge; an evident middorsal keel; plane from marginal edge to plastron concave (Fig. 3).

Adults typical of short-necked chelids in ventral aspect. Bridge short (mean=.22 of carapace length); plastron shorter (mean=.76 LC) than any other Australian short-neck, anterior plastral edge not extending to anterior edge of carapace, not visible in dorsal view; anterior lobe of plastron distinctly tapered, posterior lobe only slightly tapered. A distinct, wide, posterior plastral notch.

Precentral [nuchal] scute always present. Interlateral-marginal seam contacts (see Fig. 1 for explanation of terminology): A1 unknown; C6 rare; D9 common (67%); E113 common (91%, highest frequency of any Australian chelid). Intergular scute wide (mean=.08 LC), wider than any short-necked Australian chelid except *Elseya latisternum* and *Pseudemydura umbrina*. Central [vertebral] scute C5 short (mean=.16 LC); C1 through C4 wide (means = .17, .26, .26, .24 LC, respectively). Anal scute is longest plastral scute in all immature specimens examined. In the four adult types the anal is the third longest. Observed plastral formulae: Pec>Fem>An or (Fem≈Pec)>An in adults; Fem>(Pec≈An) in all non-adults (Fig. 7).

Shell smooth, unserrated, and indistinctly keeled at hatching; marginal serrations develop in second month, usually become extreme in first year and persist throughout all immature stages (to about 200 mm); middorsal keel serrated in lateral profile; marginal serration and middorsal keel completely lost in large adults; middorsal line of adults often depressed. Carapace scutes imbricated in immature animals, not in adults. Juveniles develop pattern of radial ridges on carapace scutes; ridging on adult scutes longitudinal, only vaguely radial; both kinds of ridging may be related to growth phenomena. Little or no pathological shell pitting

Table 1. Measurements (mm) and live weights (g) for *Elusor macrurus*. Where no museum number is given, specimen is live in a private collection. Abbreviations: m, male; f, female; im, immature; mim, male immature; fim, female immature; juv, juvenile; LC = carapace length, WC = carapace width, LP = plastron length, HT = depth of shell, WT = weight, WH = width of head.

Specimen	Sex	LC	WC	LP	HT	WT	WH	Remarks
QMJ 51273	m	378	273	305	108	5500	46.5	Live Paratype
QMJ 51274	m	347	241	293	101	3800	41.0	
AMR 134981	f	326	230	273	108	3440	44.5	
QMJ 51275	f	312	235	268	102	3150	40.2	Holotype
—	fim	251	198	202	68	—	32.6	
UU 19488	im	220	171	187	69	—	27.7	
UU 19486	mim	192	161	154	56	595	26.5	
UU 18007	mim	160	139	126	48	412	24.6	
—	im	111	100	83	39	—	17.3	
UU 18005	juv	46.4	43.7	33.6	17.6	—	10.4	
QMJ 51468-70, 54138-40	juv	32.2	30.3	—	—	6.76	—	Mean for 6 neonate sibs

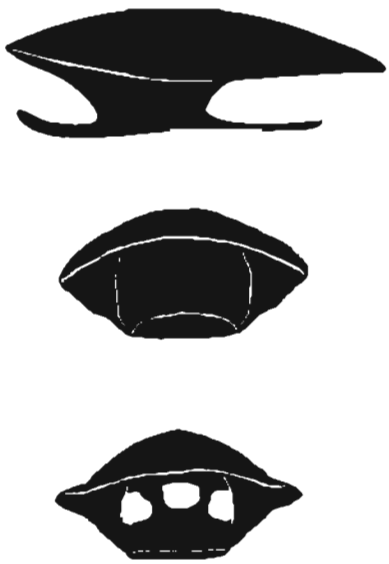

Figure 3. Profiles and optical cross-sections of *Elusor macrurus*. Upper: AMR 134981, female, LC 326 mm; Middle: same specimen, WC 230 mm; Lower: UU 19488, immature, WC 171 mm.

of the kind described for *Rheodytes*.

Soft Parts. — Skin of soft parts typically chelid, lacking the rough "sandpapery" feel of *Rheodytes*. No rostral pores; no follicular tubercles. Musk gland ducts opening ventrally at level of M3-4 anteriorly and M7-8 posteriorly where soft skin joins marginal scutes. Webbing on feet soft, flexible, and extensive. Cloacal bursae with proximal half (part closest to orifice) of lining covered by flattened bladelike papillae, some of which are branched.

Skin of ventral head and neck unremarkable, like most other short-necked chelids, soft and bearing a series of creases that seem to delimit triangular or diamond-shaped scales; no plaquelike scales, no micropustulate topography.

Eye. — Eye dull, dark, and unpatterned; pale ring absent or vague in adults. An evident vestige of a nictitating membrane covering 10 to 20% of eye. Eyelid slightly translucent (Fig. 4).

Head. — Lateral head profile distinctive; contribution of soft snout outline less than contribution of anteriormost part of maxillary sheath (snout much more prominent in *Rheodytes*); square-fronted, not low and tapered from level of barbels to area just below snout. Head narrow (mean=.16 LC); cross section of head rounded on top, widest at upper level of tympanum, not straight-sided; no prominent overbite of maxilla in profile; bony orbit small (mean=.039 LC); mandibular symphysis short (mean=.037 LC) (Figs. 4 and 6).

Tomial edge of maxillary sheath straight in profile, not curving upward from front to rear, not forming a "smile"-like outline. In anterior view of large adults, maxillary tomial sheath flares slightly outward from vertical plane of mandibular tomium, producing an overlapping occlusion reminiscent of large-headed *Emydura* (Fig. 4).

Headshield distinct, smooth, cornified, and darker than dorsal ground color at all ages but becoming more distinct with age; shield begins on posterior snout at level of anterior orbital rims and extends back to posterior extent of dermal skull roofing; quadrilobate in adults with slight, lateral earlike extensions at level of posterior third of tympanum; triangular in immature specimens; darker mottling usually present.

Postorbital and temporal scales (in region bounded by headshield and edges of tympanum) distinct and plaquelike, tending to be irregularly rounded or oval but elongated in some cases. Scales smooth and soft, not keratinized, not micropustulate, seemingly not becoming gnarled or hard with age. Skin of tympanum unscaled, at most scored with irregular lines or creases.

Dorsal palatal surface of mouth virtually identical to *Rheodytes*; maxillary triturating surfaces narrow, almost totally reduced in premaxillary region where they bound a prominent vascular, tumescent pad. A possible "median alveolar ridge" weakly developed on mandibular and maxillary triturating sheaths, not visible on underlying bones; ridge consists, at most, of 4 to 5 very small tubercles and is clearly visible only with special light and magnification.

Tongue simple and triangular, bearing no evident integumentary specializations other than simple transverse plicae.

Neck. — Neck tubercles in two longitudinal dorsolateral series, in which five to seven transverse whorls are

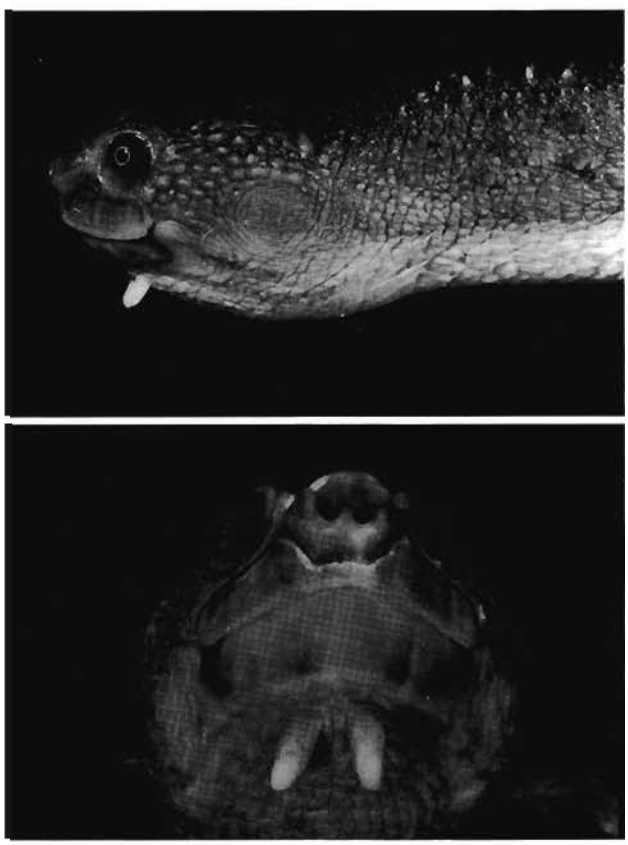

Figure 4. Heads of *Elusor macrurus*. Above: male paratype, QMJ 51273. Below: female paratype, AMR 134981, showing largest barbels observed.

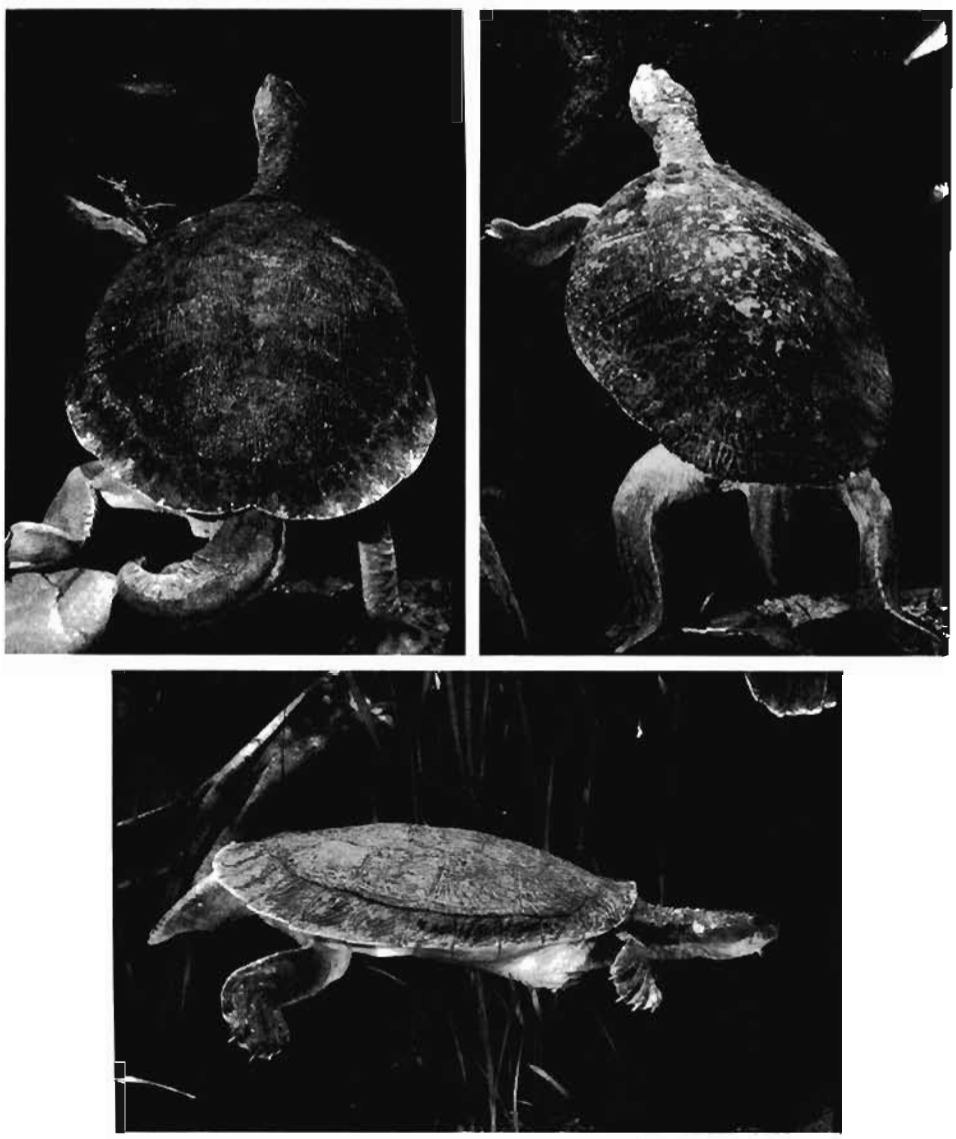

Figure 5. Tail shape and size in live *Elusor macrurus*. Top left: male paratype, QMJ 51273; Top right: female paratype, AMR 134981; Bottom: immature, LC 245 mm. Note the extremely short postcloacal part of the tail and its great depth in immature specimen.

vaguely distinguishable. Tubercles of intermediate development (neither the spiky cones of *Elseya latisternum* nor the small blunt tubercles of *Emydura*). Shape of tubercles in juveniles blunt to pointed, two-thirds as wide as long; tubercles blunter and shorter in adults.

Usually four chin barbels; one large median pair between two much smaller lateral barbels. Median barbels large and fleshy, 5 to 10 mm long, length 1.7 to 2.8 times basal diameter in adults. Never a single median barbel.

Tail. — Cloacal orifice a longitudinal slit; precloacal part of tail heavily developed in all individuals, always longer than postcloacal part. Cross section of tail a vertical ellipse (both precloacal and postcloacal parts). Total length of tail up to 70% of carapace length in large males. Posterior edge of cloaca nearly always posterior to rear edge of carapace, tip of tail always so. Tail lacks enlarged ventral scales. A median dorsal raphe (up to 0.5 mm high) on posterior third of tail.

The long massive tail is the most striking feature of an adult male. It is almost the mass of a small human wrist (Fig. 5). Distal muscular part of tail begins ventrally at midcloaca. Proximal, precloacal part of tail dominated by a huge ventral swelling which presumably accommodates the penis; swelling terminates at midcloaca with a pair of subordinate swellings, each of thumb-tip size, on either side of cloaca; subordinate swellings covered with distinctive plaquelike scales and distinct in texture from rest of tail (also present in holotype but smaller); swellings clearly visible in dorsal view of tail.

Osteology

Skull. — A well-developed retroarticular process on mandible. Splenial bone present as a distinct separate ele-

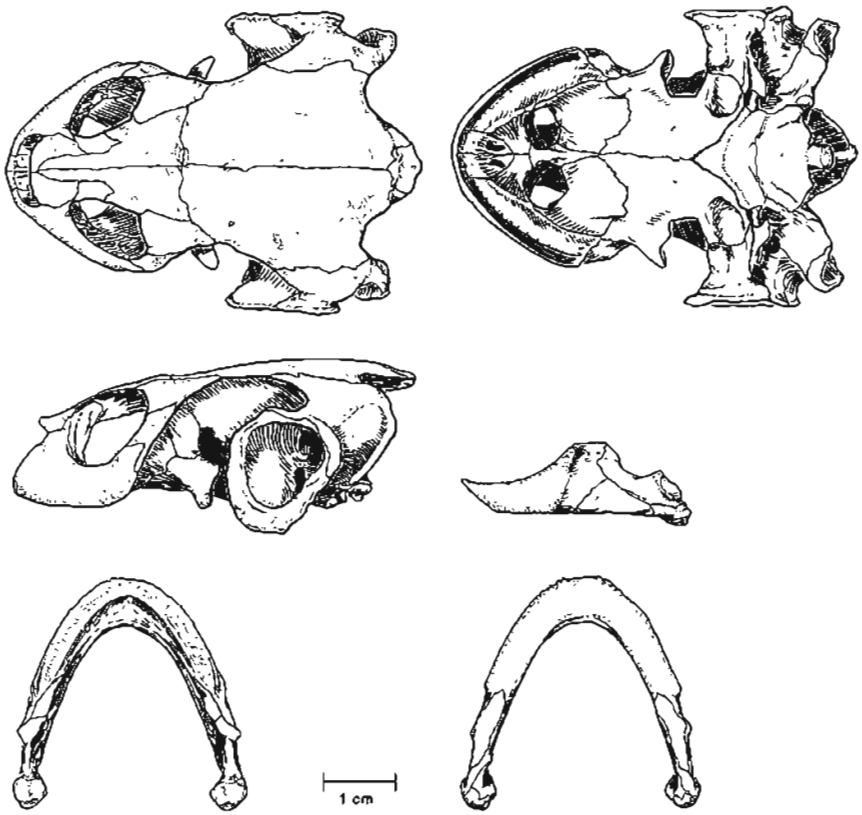

Figure 6. Cranium and mandible of *Elusor macrurus*, AMR 134981, condylobasilar length 52 mm.

ment of lower jaw. Dentary symphysis co-ossified in adults, never visible. Prefrontals and nasals in contact, excluding a maxillary-frontal contact on dorsal exposure of skull. Prefrontals broadly exposed on anterior part of dorsal orbital rim. Ventral processes of prefrontals not closely approximated, not constricted, permitting virtually unobstructed view posteriorly through fissura ethmoidalis. Ventral ridges of frontal bones vertical, not turned inward, not closely approximated. Temporal roof only slightly emarginate posteriorly. Horizontal plate of supraoccipital forming a small, dorsally exposed plate of bone at posterior edge of skull roof. No posterior projection of supraoccipital spine. Skull of *Elusor* illustrated in Fig. 6, with comparison palatal views of *Rheodytes*, *Elseya latisternum*, and *Elseya dentata* in Fig. 9.

Shell. — Entoplastron relatively broad (W 29.4 mm, L 32.5 mm), pentagonal in disarticulated internal and external exposures; anterior end nearly straight-sided, not pointed. Internal exposure shows broad anterior head, distinct lateral wings, and a distinct posterior tail; lateral wings straight and horizontal. Gular scutes do not overlap entoplastron; intergular scute covers entire width of anterior end.

Inguinal buttress nearly as large as axillary buttress and of similar structure in frontal section; posterior part of sternal cavity almost as commodious as anterior part. Rib tips of costals 2 to 4 form articulations in or near interperipheral sutures, never in or near centers of peripherals. Shell of *Elusor* illustrated in Fig. 7.

Neck and Limbs. — Neck relatively short, sum of cervical centra 2 through 8 is .35 of carapace length. Femur short (.20 LC), humerus and femur of subequal length (.19 and .20 LC, respectively).

Tail. — Three normal tail skeletons were examined: AMR 140845, adult male, complete tail skeleton from incomplete skeleton, carapace length 349 mm (tail 245 mm); AMR 134981, female paratype, 326 mm (tail 127 mm); NMV D-55457, immature, 134 mm (tail 58 mm). Tail x-rays of two live males established the relationships of the cloaca

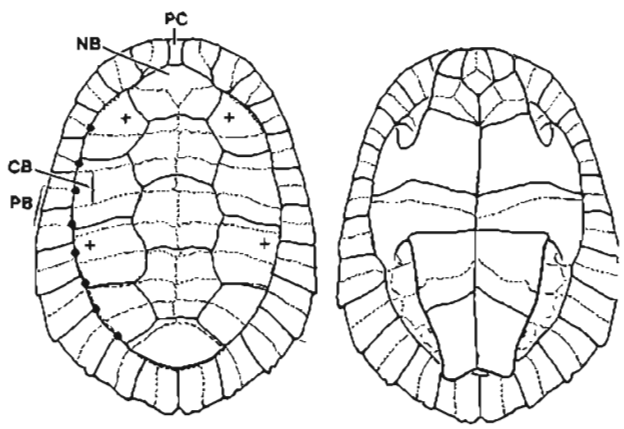

Figure 7. Dorsal and ventral views of scuteless shell, *Elusor macrurus*, immature, NMV D-65881, LC 219 mm. Crosses show approximate locations of ends of buttresses; dots show approximate positions of rib tips. Abbreviations: CB, costal bone; NB, nuchal bone; PB, peripheral bone; PC, precentral [nuchal] scute.

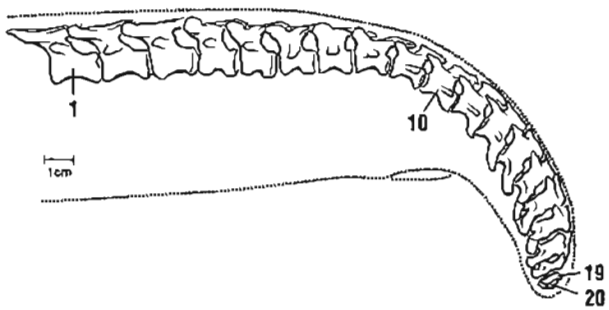

Figure 8. Isolated and probably incomplete tail skeleton, *Elusor macrurus*, AMR 140845, adult male, LC 349 mm. Numbering of vertebrae is arbitrary but probably accurate. Dotted lines show soft structure of tail with cloacal orifice. Note haemal arches on ventral aspect of distal vertebrae.

to the tail skeleton. On none of the tail skeletons was it possible to determine if all the postsacral vertebrae were present. For practical purposes, it was assumed that the terminal vertebra was # 20 and the remaining vertebrae were numbered from this reference point.

A description of a male tail skeleton (AMR 140845) follows (see Fig. 8). Vestiges of haemal arches occur irregularly as single or paired processes indistinguishably fused to the centrum on caudal vertebrae 3-9. The laterally compressed postcloacal part of the tail contains caudal vertebrae 11-20. Haemal arch 11 aligns with approximate center of cloacal orifice. Haemal arches fairly distinct and fused to centrum but members of a pair not fused ventrally on 10-11. Haemal arches very long and distinct on 12-13. Caudal vertebrae 14-18 are laterally compressed and their centra have lost the distinctive spool shape. Haemal arch 14 is double and its members are fused ventrally. Haemal arch 14 joins haemal arch 15 by a ligamentous joint; the haemal arch of 15 is fused to its centrum. Caudal vertebra 16 has a distinct non-fused haemal arch which has a ligamentous attachment to haemal arch 17. Caudal vertebrae 19 and 20 lie in the extreme tip of the tail, are greatly reduced and bear little resemblance to vertebrae of any kind. The tops of neural arches 9 through 19 form long, narrow, gnarled plates of bone which seemingly fuse to the dorsal skin of the tail. Similar plates are less distinctly developed on haemal arches 11 to 19.

Coloration

Adults. — The coloration of adults (preserved or live) is dull, unpatterned, and in no way spectacular or distinctive when compared to most other Australian short-necked chelids. Dorsal aspect blackish-brown to neutral, nondescript, homogeneous dark color, in some cases, small scarlike areas of grayish horn color. Ventral aspect almost totally grayish on soft parts and chiefly grayish to darker slate on plastron and inframarginal surfaces. Vague flesh colored areas straddling the interosseous sutures (visible through the scutes). Total range of color in ventral view is slate or pearl gray to cream. There is no discernible plastral pattern in adults; on the holotype there is vague dark mottling on some of the plastral scutes and on the inframarginal surfaces. On the AMR female paratype there is a definite reticulated, possibly modified radial, pattern on inframarginal surfaces 4-7 and to a lesser extent on 10-12. This brown reticulation is reminiscent of that seen in *Elseya dentata* from the Gulf of Carpentaria drainages.

Preserved Juveniles. — In most juveniles there is extensive dark coloration ranging from solid smudges to mottling on the enlarged inframarginal surfaces. Dorsal surfaces of the soft parts are dull, slightly brownish slate in all preserved specimens; less dull and less dark in immature specimens than in the largest adults. The contrast between ventral and dorsal coloration on head and neck is much greater in juveniles than in adults, but a sharply bicolored condition does not exist at any stage in *Elusor*. The head shield exists as a discrete and distinctively colored cornified region, significantly darker than the soft skin at all ages. Many preserved juveniles are in poor condition and it is difficult to discern a carapacial pattern; in one juvenile there is a radial pattern of dark brown on paler amber-brown, the radiations being much like the dark lateral radiations of *Elseya latisternum*.

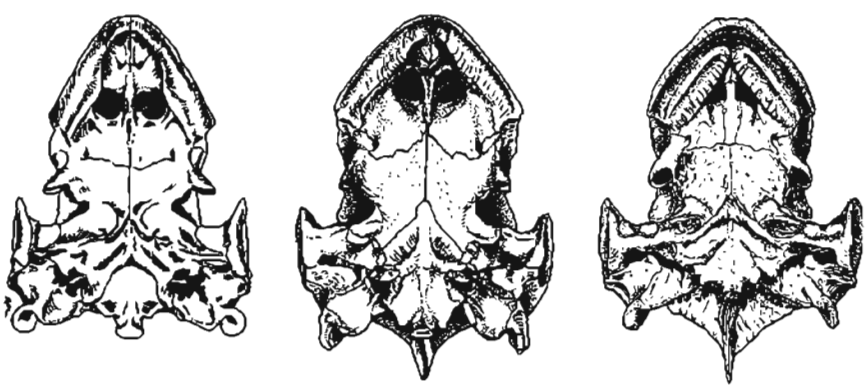

Figure 9. Palatal views of female skulls for comparison with Fig. 6. Left: *Rheodytes leukops* (UU 17114), Center: *Elseya latisternum* (UU 15258), Right: *Elseya dentata* (UU 17877). Condylobasilar lengths 42, 58, and 61 mm, respectively.

Live Hatchlings. — Color within a few days of hatching is as follows. Carapace dark olive to almost black flecked with fawn, chiefly on the lateral scutes (some flecking on marginals and central scutes). Plastron pale gray with a bluish tinge. Ventral soft parts pale gray suffused with pink. Claws grayish and pale-tipped. Dorsal soft parts darker gray. A pale stripe from the angle of the mouth onto neck, fading under tympanum and then becoming distinct again on side of neck.

The following dramatic changes occur at about three weeks. Predominant ground color ranges from fawn to various shades of brown or dark to medium olive. Lateral scutes and fifth central scute become paler, producing a pale U-shaped figure (bend of the U on C5, open end anterior). At this stage there is a peppering of darker patches on carapace. Eye with distinctive inner pale ring (which usually disappears later in ontogeny). Pale U-shaped figure supplanted by the uniform darker ground color within eight months. Henceforth plastron and inframarginal surfaces become progressively paler and suffused with pink.

Live Older Juveniles. — Basic ground color of carapace medium brown, suffused or not with rosy pigment, often horn-colored at free edges, especially posterior edge; darker brown radial marking on each scute increases with age; interlaminal seams not distinctly darkened; often a narrow, pale peripheral ring on edges of marginals; osseous sutures visible as paler lines through epidermal laminae.

Ground color of plastron ranges from pale slate gray to neutral cream, which may be suffused with various amounts of rosy pigment. Pale ground often broken by vague patches of slate color associated with edges of posterior plastral fontanelle. Inframarginal surfaces essentially same color as plastron, often with slate flecks. Larger subadults with pinkish ventral coloration; interosseous sutures may contrast as pale yellow through translucent scutes. No darkening of interlaminal seams and never a distinct or bold plastral pattern.

Ventral ground color of soft parts has same range of color as plastron; pinkish or orangish coloration tends to be concentrated on individual limb scales with intervening smaller scutes more nearly dull and neutral. Ventral surface of tail often shows brightest pinkish orange of any part of ventral view. Tail usually has a dark dorsal or two dark dorsolateral longitudinal stripes. Dorsal ground color of soft parts darker, brownish, usually uniform, but there is no sharp distinction or contrast between dorsal and ventral fields. Dorsal head and neck darkest neutral brown with irregular radial flecks of dark brown or black on head shield. Usually no rosy coloration on head and neck except neck tubercles and barbels.

Eye in general is somber and dark, never bright. Eye coloration consists of a narrow pale (sparkling gold) ring bordered immediately by a field of mottled black and then extremely dark olive brown. The ring may be visible only under magnification. Never a bright wide ivory ring as in *Rheodytes.*

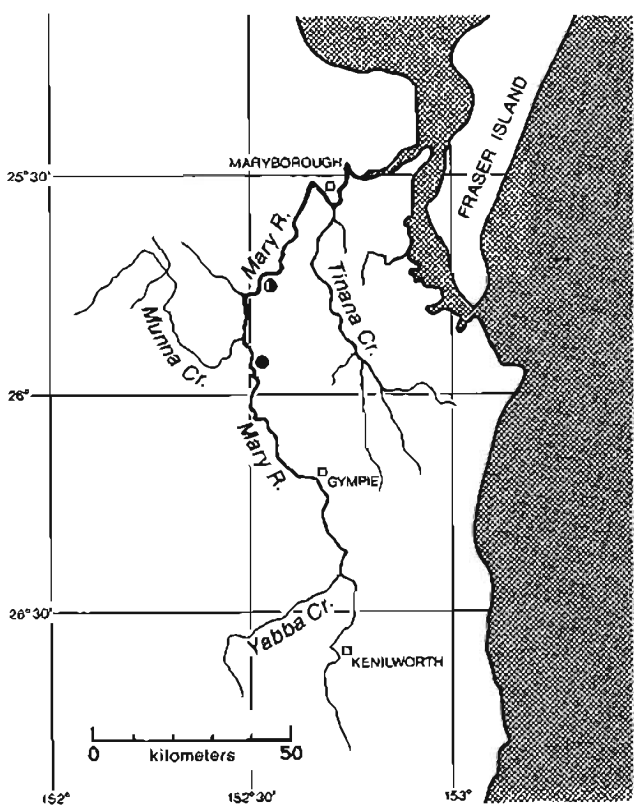

Figure 10. Map of the Mary River drainage in southeastern Queensland showing the only localities from which catalogued museum specimens exist. Solid dot, type locality; half dot, adult paratypes.

Geographic Distribution

Information from all reliable sources indicates that *Elusor* occurs at least from the latitude of Gympie to the tidal reaches of the Mary River, upstream from Maryborough, and probably nests in suitable places along those parts of the river (Figs. 10-11). Cann has personally seen *Elusor* at various localities between latitudes 26°00'S and 25°40'S. *Elusor* probably occurs in all the deeper holes of the Mary River downstream from Kenilworth (20°35'S, 152°46'E).

There is no evidence that *Elusor* occurs anywhere outside the Mary drainage. We have done a substantial amount of work (including diving) in the Brisbane and Burnett rivers without seeing *Elusor.*

The mouth of the Mary River is near Maryborough and its delta lies in the narrow strait between the mainland and Fraser Island. The river flows northward from the approximate latitude of Conondale (26°44'S, 152°43'E) on the northeast face of the Conondale Range, approximately 85 km NNW of Brisbane City center. The coastal plain is essentially continuous from Tweedheads (28°12'S) to the region of Innisfail (17°30'S) although it narrows substantially near Mackay, Gladstone, and just north of Brisbane. Therefore, there are no physical barriers to coastwise migration in the region mentioned.

At and near the type locality *Elusor* occurs in the same

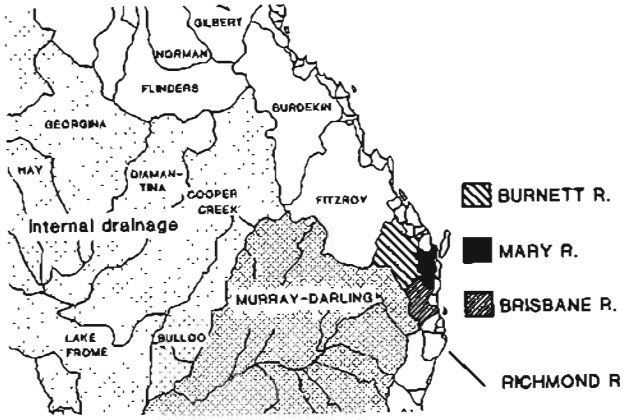

Figure 11. River drainages in southern Queensland and northern New South Wales, eastern Australia. The largest coastal island is Fraser Island.

river pools with *Emydura krefftii*, *Elseya dentata*, *Elseya latisternum*, and *Chelodina expansa*. *Chelodina longicollis* occurs nearby but chiefly in ponds and farm dams. Kenilworth (26°35'S) is probably the southern limit of distribution for *Elseya dentata* (unpublished data). Lungfish (*Neoceratodus forsteri*) are common in the river.

Rheodytes occurs only in the Fitzroy drainage. Therefore, *Elusor* bears the same sympatric relationship to the two groups of *Elseya* in the Mary River drainage that *Rheodytes* does in the Fitzroy drainage.

At present there is a barrage dam approximately 4 km NE of Mungar (25°35'S, 152°37'E) to protect water for human use from salinity. The water downstream from the dam tasted slightly salty in October 1990. Salt water fish occur in this brackish water and Cann has observed *Elseya dentata* and *Emydura krefftii* here. Freshwater creeks (e.g., Graham's Creek) probably dilute the salinity where they empty into the main river. Tinana Creek runs parallel to the Mary River and has its mouth at Maryborough. It contains some deep holes where large *Elseya dentata* occur and where the presence of *Elusor* is predicted.

During all collecting attempts in 1990 and 1991 varying numbers of *Elseya dentata*, *Elseya latisternum*, and *Emydura krefftii* were seen and caught when diving and by using traps and nets. By comparison, *Elusor* was a rarity, being seldom seen or caught. We conclude that *Elusor* is either secretive, rare at the times of collecting effort, or both.

Natural History

Habitat. — The type locality lies in cleared, heavily grazed cattle country (Fig. 12). There are fences on both sides just above flood level (ca. 14 m). The fences on opposite banks are approximately 300 m apart. The river itself varies from 60 to 100 m in width but is significantly narrower in places. Rocks protrude from the banks or jut from the water, creating turtle basking platforms. There is a minimum of dead wood in the water. The water is now always brown and turbid because of increasing commercial sand-mining upstream. Water visibility in October 1990 was approximately 1.2 m near the surface. In October 1991 visibility was far less and the river was at its lowest level in history because of severe drought. Little aquatic vegetation is present in this part of the river. The greatest depth measured near the type locality was 3 m. The holotype and allotype were taken by diving at depths of 1.5 to 2.0 m.

Turtle habitat is less disturbed at the downstream locality where the paratypes were taken (Fig. 12). Here the river is wider, deeper (5 m), there is more dead wood in the water and the streamside vegetation is more nearly natural. Flow in all parts of the river is generally slow.

Size and Growth. — *Elusor* may attain the largest adult size of any short-necked Australian chelid. Adult sizes shown in Table 2 rank with *Elseya dentata* and the larger species of *Emydura*.

Carapace lengths and widths of four hatchlings within a few hours of hatching were (mean and range, in mm): 34.8 (32.5-36.5) x 31.8 (30-32.5). Most captive hatchlings in Sydney reached a carapace length of approximately 53 mm in 11 months but some grew to as much as 100 mm carapace length.

Since most of the immature specimens examined were captives of unknown provenance, natural rate of growth and

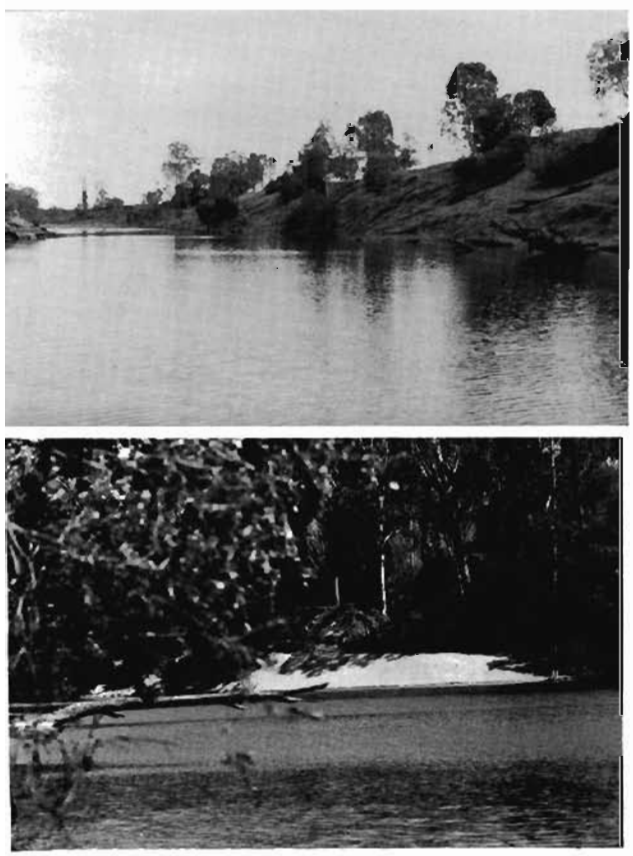

Figure 12. Habitat of *Elusor macrurus*, Mary River, Queensland. Top: the type locality in disturbed grazing land, December 1991. Bottom: locality where paratypes were obtained, 22 October 1990. The sand bank is a known nesting beach. There is an *Elusor* adult (virtually invisible in this print) basking near the base of limb protruding from water on left.

Table 2. Maximum sizes (carapace length in mm) attained in eight generic groups of Australian chelids. Information chiefly from University of Utah database (ca. 5000 specimens). [* Based on shell from Barwon R. in private collection. ** Shell from Burnett River examined by Cann. *** Cann has observed *Elusor* estimated to be at least 400 mm basking. **** From Burbidge (1967).]

Genus	Max. LC	Males	Females
Chelodina (expansa)	485*	328	382
Chelodina (longicollis)	265	212	265
Elseya (dentata)	400**	300	374
Elseya (latisternum)	291	227	291
Rheodytes	262	262	262
Elusor	400***	380	326
Emydura	350	276	350
Pseudemydura	153****	146	142

size at sexual maturity are imperfectly known. An immature specimen of 251 mm (probably a subadult female) was judged to be 7 to 10 years old and a smaller one of 185 mm (possibly immature male) was in its fifth or sixth year, based on epidermal growth rings.

Diet. — *Elusor* is seemingly omnivorous. A freshly caught adult female passed feces containing filamentous algae and shell fragments (maximum fragment length ca. 6 mm) from bivalves up to 70 mm long (estimated by reconstructing fragments). Captives in Salt Lake City are fed a diet of beef heart and agar-vitamin supplement; captives in Sydney receive fish, beef, and aquatic vegetation. Bivalves are common in the Mary River at the type locality; the species represented are probably *Velesunio wilsoni*, *V. ambiguus*, and *Alathyria pertexta*.

Molluscs may be an important part of the diet. The following feeding behavior has been observed repeatedly in a captive male. Bivalves up to 90 mm total length are taken into the mouth and moved about with rapid inertial feeding movements until the bivalve is aligned with the long axis of the turtle and projects from the front of the mouth. The foreclaws then rake repeatedly along the occlusal edges of the bivalve (perhaps 15-20 times). A claw is finally inserted between the occlusal edges and begins to damage the internal soft structures. At this point the bivalve "relaxes" and opens. The turtle then crushes the individual valves in the process of eating the internal soft parts. Some shell fragments are ejected and some swallowed.

We have not observed this feeding behavior in other Australian chelids and it is significantly different from the whole bivalve crushing behavior we have observed repeatedly in *Emydura* (Legler, 1981, 1984, 1989). There are no modifications of the palate or the mandible in *Elusor* for crushing hard objects (as is the case in several species of *Emydura*).

Reproduction. — Egg morphology and other reproductive characters seem essentially like those of other chelids with a southern temperate breeding pattern. Nesting occurs in late October and again about one month later and seems to be concentrated in certain favorable areas of riparian habitat (Fig. 12). In 1990 there were a few signs of turtle nesting on 16 October; after a heavy rain on the night of 17 October there was increased nesting activity (as evidenced by tracks in the sand) and by 22 October many animals were laying. Some of the tracks and nests observed could have been those of *Emydura* or *Elseya latisternum* but *Elseya dentata* breeds in the winter (May-June) (Legler, 1985). Nests were observed in sandy areas approximately 5 m above water level and approximately 30 m inland from the shoreline. Local residents who buried fresh eggs in river sand report emergence after approximately 8 weeks. Therefore the young probably emerge from natural nests for at least a month beginning in late December.

Seventeen eggs were removed from six nests at various localities along the river on 16 October 1990. Mean dimensions and extremes (in mm) were: 34.8 (34.0-37.0) x 23.6 (22.5-25.0). The eggs have thin flexible shells and can swell in the course of incubation. Nests observed by Cann contained 14 to 15 eggs each. Local residents report maximum clutch size as 25.

Behavior. — Mature males are aggressive and cannot be kept in the same aquaria with other males of the same species. Despite this, individuals of *Elusor* are easy to handle and seldom attempt to bite (unlike most other shortnecks).

Elusor seems to shun baited traps and thus far has been caught chiefly by diving. Cann regards *Elusor* as the fastest shortneck. *Elusor* demonstrates cloacal pumping but regularly breathes at the surface. Captives cruise the surface and seem to go through the motions of neustophagia. In the wild, heads have been observed at the surface and basking is common. Captives spend much of their time resting at an angle, at neutral or slightly positive buoyancy, with the tip of the snout at or near the surface. Normal shedding of whole scutes occurs. Grooming (Putzverhalten) has not been observed. *Elusor* shares these behavioral characteristics with *Elseya latisternum* and *Elseya dentata*. By contrast, *Rheodytes* seldom surfaces to breathe, maintains negative buoyancy, is an efficient bottom walker, grooms on a regular basis, does not shed whole scutes, and does not bask.

The allotype and female paratype have various amounts of epizoic algae on the shell and headshield. Legler and Cann (1980) remarked on an unusual gregarious clumping of sibling hatchlings in *Rheodytes*. We were unable to induce this behavior in the hatchling *Elusor* available to us.

DISCUSSION OF CHARACTERS

Buttresses. — A buttress is a dorsal extension of a plastral element (hyoplastron = axillary buttress, hypoplastron = inguinal buttress) lying in a parasagittal plane. In most chelids the axillary buttress is augmented by a transverse plane of bone that joins the the main buttress at an obtuse or right angle. This osseous angle embraces the anterior sternal cavity. In *Elseya dentata*, *Elseya latisternum*, and *Emydura* the inguinal buttress is less extensive than the axillary (hypoplastron contributes less than hyoplastron to bridge), there is no posterior, transverse bony plane comparable to that of the axillary buttress, and the posterior sternal cavity is not embraced by an osseous angle. In *Elusor* and *Rheodytes* the hyo- and hypoplastra contribute almost equally to the

bridge, the anterior and posterior sternal cavities are of subequal size, and the inguinal buttress bears a posterior plane of bone comparable to that of the axillary buttress. These features in *Elusor* are all slightly less extreme than in *Rheodytes*.

Cloacal Bursae. — All Australian chelids have cloacal bursae with at least some modification of the bursal lining in the form of vascular rugae or papillae that increase the internal surface area. The cloacal bursae can function as cloacal gills (Legler, 1993b; Legler and Georges, 1993). In *Elusor* the proximal half of the bursal lining (closest to the orifice) is covered by bladelike papillae, some of which are branched. This degree of specialization is close to that of *Elseya latisternum* and *Emydura*. In *Rheodytes* and *Elseya*, on the other hand, the bursal lining is completely covered with long, branched papillae. In *Rheodytes* the papillae and their branches are conical; in *Elseya dentata* they are flattened and bladelike.

Eye. — Eye coloration in chelids is usually contrasting (a pale iris on a darker background) and may be bright (see Fig. 6 in Legler and Cann, 1980). Contrast and brightness are often secondarily modified (probably camouflaged) by a stellate pattern of radial dark marks intersecting the pupil and the periphery of the eye (e.g., *Elseya latisternum* and *Chelodina oblonga*). The bright eye of *Rheodytes leukops* is never stellate. At the other extreme, adults of *Elseya dentata* have a dark somber eye with little contrast. Eye coloration in *Elusor* most closely approaches that of *Elseya dentata* but in some adults of *Elusor* (Fig. 4) a narrow pale ring persists.

Australian chelids lack nictitating membranes and Harderian glands but have well-developed lachrymal glands. There may be a small vestige of the nictitating membrane in *Emydura*, *Elseya latisternum*, and in *Elseya dentata*, but seemingly never in *Rheodytes*, *Pseudemydura*, or *Chelodina*. The eyelid is translucent to virtually transparent in Australian chelids. Eyelid transparency is definitely greater in taxa without trace of the nictitating membrane. In some young chelids (e.g., *Chelodina longicollis*) the eye can be seen clearly through the eyelid and the eyelid seems to be functioning in lieu of a nictitating membrane. *Elusor* demonstrates the most extensive nictitating membrane and the least translucent eyelid of any chelid studied and, in this character, is most like *Elseya dentata* (all information on eye anatomy, Legler, 1993b; Legler and Georges, 1993).

Tail. — The tail is the most distinctive feature of *Elusor*. Its lateral compression is evident in individuals of all ages and the number and structure of the caudal vertebrae is virtually identical in adults of both sexes and juveniles (data from three specimens, see "Osteology" above). The tail of mature males differs chiefly in size (length up to 70% of carapace length, dry weight of tail skeleton slightly exceeds weight of skull and mandible).

Tail comparisons among Australian chelids were extensive; 60 dry tail skeletons of 6 genera were examined (see Table 3, only *Pseudemydura* lacking). Caudal vertebrae of a few other pleurodires were also examined: Chelidae – *Chelus fimbriatus* (2); *Hydromedusa tectifera* (1); *Phrynops geoffroanus* (1); *Phrynops gibbus* (1); *Platemys platycephala* (3); Pelomedusidae – *Pelomedusa subrufa* (1); *Pelusios* sp. (2).

Haemal arches were not found in any other Australian chelid. Among the other pleurodires, small haemal arches were found only in *Chelus*. Tail skeletons of *Platysternon megacephalum*, *Chelydra serpentina*, *Macroclemys temminckii*, and *Clemmys marmorata* were also examined. These cryptodiran species have long, potentially prehensile tails and all have haemal arches to varying degrees. However, in all of the pleurodirans and cryptodirans examined,

Table 3. Osteological data for 8 generic groups of Australian chelids. Mean, one standard deviation of the mean, and extremes are expressed where N is greater than one.

Taxon (n)	Sum Cervical Centra 2-8/LC	L. Humerus/LC	L. Femur/LC	No. Caudal Vertebrae
Chelodina expansa (11)	.752 ± .041 (.68-.81)	.191 ± .008 (.18-.21)	.241 ± .007 (.23-.25)	19 (17-22)
Chelodina longicollis (10)	.619 ± .040 (.52-.64)	.198 ± .008 (.18-.21)	.248 ± .007 (.24-.26)	19 (16-21)
Elseya dentata (9)	.346 ± .023 (.32-.38)	.191 ± .015 (.17-.21)	.223 ± .017 (.20-.24)	21 (17-23)
Elseya latisternum (10)	.415 ± .017 (.38-.44)	.192 ± .008 (.18-.20)	.230 ±.008 (.21-.24)	20 (17-23)
Rheodytes (10)	.411 ± .015 (.39-.43)	.197 ± .007 (.18-.21)	.254 ± .012 (.24-.27)	18 (16-21)
Elusor (2)	.345	.186	.205	21 (21-22)
Emydura krefftii (10)	.373 ± .018 (.35-.41)	.178 ± .008 (.17-.19)	.215 ± .012 (.20-.24)	21 (17-23)
Pseudemydura	.42	.22	.24	No data

the cross-section of the tail is rounded or rounded-rectangular, the tail tapers to a pointed tip and the vertebral centra are spool-shaped.

The presence of haemal arches in *Elusor* is therefore unique among Australian chelids and the lateral compression of the distal caudal vertebrae and the lateral compression of the tail may be unique among turtles generally.

The function of the tail is not clear. The extreme hypertrophy of the tail in adult males suggests a function associated with mating. Lateral compression of the postcloacal tail suggests a paddlelike or rudderlike device. The ventral curvature of the tail skeleton (Fig. 8) suggests prehensility.

Observations of captives in aquaria and swimming pools did not elucidate tail function. During normal to rapid aquatic locomotion the tail may be dragged passively, moved from side to side in a motion that vaguely resembles sculling, or tucked in beneath the rear edge of the shell. Other shortnecks do these things to some extent. A large captive male in Sydney repeatedly used the tail in a powerful thrashing motion when attempting to crawl out of an aquarium during feeding.

Neck and Limbs. — Neck length in Australian chelids has been used subjectively and colloquially to express evident differences between major groups ("longnecks" and "shortnecks"), but is usually not expressed quantitatively. The lengths of the centra of cervical vertebrae 2 to 8 were measured and added. The resulting sum was expressed as a percentage of carapace length (Table 3). Cervical vertebra 1 was not considered because it consists of separate loosely articulated elements in the shortnecks. In the genus *Chelodina* cervical centra 2-8 equal more than half the length of the carapace (*much* more if C1 is added in), whereas in the shortnecks the sum is significantly less than half. Within the shortnecks there are two subgroups of neck length; *Rheodytes* and *Elseya latisternum* have relatively long necks (ca .41 of carapace length) whereas *Elseya dentata*, *Elusor*, and *Emydura* have relatively short necks (.35, .35, .37 LC, respectively). This discrepancy in neck length is evident in live animals moving about freely in aquaria.

The femur is much longer than the humerus in most Australian chelids (see Table 3). In *Elusor*, the two bones are of subequal length. The femur, expressed as a percentage of carapace length, is shorter in *Elusor* than in any other Australian chelid.

SYSTEMATIC RELATIONSHIPS

Gaffney (1977) regarded *Pseudemydura* as the most primitive member of the Family Chelidae and placed all *Emydura* and *Elseya* (*Rheodytes* and *Elusor* were not yet known) as the sister group of the remaining chelids. Our analysis, after using *Chelodina* as an outgroup, considers only Australian short-necked chelids. We interpret the assemblage of *Emydura*, *Elseya*, *Elusor*, and *Rheodytes* as monophyletic, with *Pseudemydura* representing a distinct and separate lineage.

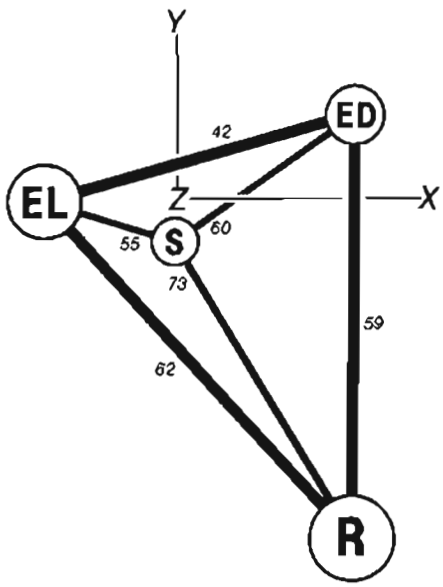

Figure 13. Three-dimensional scatter plot showing mean centroids of four short-necked generic groups based on 942 specimens of all sizes and ages (EL= *Elseya* (*latisternum*) generic group, n=526; ED= *Elseya* (*dentata*) generic group, n=302; R= *Rheodytes*, n =73; S= *Elusor*, n=41). The X, Y, and Z axes are canonical axes generated in a BMDP7M stepwise discriminate analysis and then plotted with JMP. The BMDP analysis was based on 31 chiefly mensural characters (excluding carapace length, see Methods and Materials). Coordinates for centroids are exactly as plotted by JMP but spheres and intercentroid lines are added to suggest depth. The Z axis extends from plane of illustration toward viewer. Numbers on interconnecting lines represent approximate intercentroid distances measured in mm on plots rotated to maximize distance between each pair.

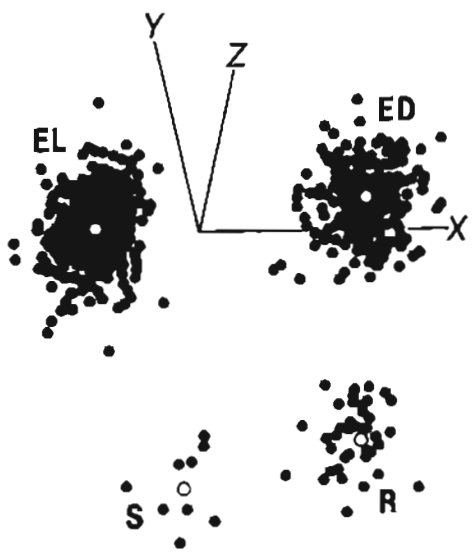

Figure 14. Three-dimensional scatter plot of 582 adults superimposed on mean centroids shown in Fig. 13. The plot has been rotated (in JMP) 5° to the right on the Y axis and 20° upward on the X axis (Z axis now projects upward and to the right) to maximize the separation of clusters on a single plane. Also, the plot has been "exploded" in JMP for clarity, without altering the relative positions of the points. There is no statistical or visual overlap of these clusters even when all 942 individuals are plotted. The few outliers are associated with the closest centroid. Sample size: *E. dentata*, 181; *E. latisternum*, 355; *Rheodytes*, 37; *Elusor*, 9. Abbreviations as in Fig. 13.

Elusor shares characters with most other short-necked Australian chelid genera (Table 4) but its distinguishing characters, in our judgement, warrant its placement in a new genus. Previous subjective judgements of relationships within the short-necked Australian genera are stated in Legler (1981, 1984, 1989) and Legler and Cann (1980). *Emydura* was regarded as the sister group to the remaining non-*Pseudemydura* genera. The remaining "*Elseya* group" was regarded as a monotypic assemblage of four related but distinct genera [*Elseya* (*dentata*), *Elseya* (*latisternum*), *Rheodytes*, and *Elusor*]. The multidiscriminate analysis presented in this paper shows an equidistant juxtaposition of these genera and suggests a roughly equal degree of relatedness *inter se* (Figs. 13-14).

A preliminary cladistic analysis produced somewhat different results. The *Elseya* (*latisternum*) and *Elseya* (*dentata*) generic groups emerge as much less closely related than we had originally hypothesized. The *Elseya* (*latisternum*) group is clearly placed as the sister group to all other non-*Pseudemydura* shortnecks, and *Emydura* is the sister group to all remaining members of the "*Elseya* group" (Fig. 15). Therefore, perhaps *Elseya* (*latisternum*) should not be regarded as a member of the "*Elseya* group" at all.

Georges and Adams (1992) regarded *Elusor*, *Rheodytes*,

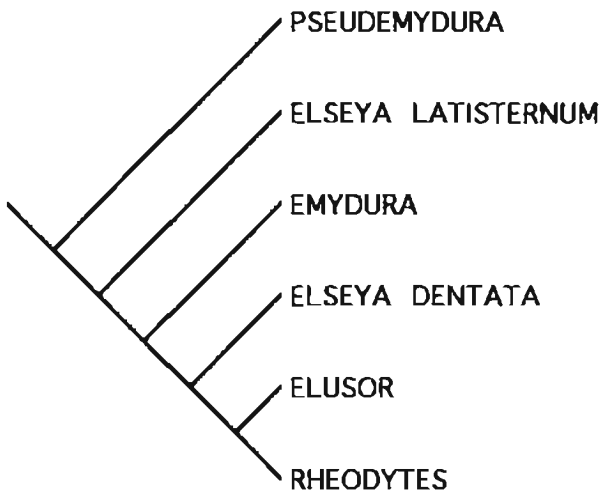

Figure 15. Cladogram generated in PAUP 3.0, showing the 6 genera of short-necked Australian chelids hypothesized in this paper, based on 35 morphological characters (see Table 4) and 16 allozymes (from Georges and Adams, 1992). The characters are unordered and of equal weight. Tree length 61; consistency index 0.98.

Table 4. Characters (51) and character states used in the construction of the cladogram in Fig. 15. Characters 1-35 result directly from Legler's work on chelids. Characters 36-51 are allozyme states from Georges and Adams (1992). Invariate allozyme characters were omitted.

	CHARACTER	*Elseya dentata*	*Elseya latisternum*	*Rheodytes*	*Elusor*	*Emydura*	*Pseudemydura*
1	Median alveolar ridge of maxilla	present	absent	absent	absent	absent	absent
2	Temporal roofing	ventral emargination	ventral emargination	ventral emargination	ventral emargination	ventral emargination	extensive
3	Ventral ridges, frontal bone	parallel and vertical	turned sharply inward	parallel and vertical	parallel and vertical	parallel and vertical	turned sharply inward
4	Fissura ethmoidalis	broad	broad	keyholelike	broad	broad	broad
5	Dentary symphysis	co-ossified	sutural	co-ossified	co-ossified	co-ossified	co-ossified
6	Splenial bone	reduced or absent	present	absent	reduced	reduced	reduced
7	Prefrontal: dorsal exposure	extensive	extensive	reduced	extensive	extensive	extensive
8	Maxillary-frontal contact	no	no	yes	no	no	no
9	Serration of rear edge of carapace	juveniles only	juvs. and adults	juveniles only	juveniles only	never	never
10	X-section of rear edge of carapace	thin and sharp	thin and sharp	thin and sharp	thin and sharp	thin and sharp	thick and blunt
11	Plastral buttresses	axillary larger	axillary larger	equal size	equal size	axillary larger	axillary larger
12	Plastral coverage of of shell outlets	normal	normal	normal	normal	normal	extreme
13	Sternal index (see methods)	>1000 cc	500-800 cc	500-800 cc	500-800 cc	500-800 cc	500-800 cc
14	Tail length	normal	normal	normal	elongate	normal	normal
15	Tail X-section	rounded	rounded	rounded	lat. compressed	rounded	rounded
16	Egg size (Legler, 1985)	large	small	small	small	small	small
17	Incubation time (Legler, 1985)	long	short	short	short	short	short
18	Egg shell (Legler, 1985)	thick, brittle	thin, flexible	thin, flexible	thin, flexible	thin, flexible	thin, flexible
19	Female size at maturity (LC, mm)	>300	<200	>200	>200	>200	<200
20	Diet	herbivorous	omnivorous	carnivorous	omnivorous	omnivorous	omnivorous

Table 4. Characters and character states (*continued*).

	CHARACTER	*Elseya dentata*	*Elseya latisternum*	*Rheodytes*	*Elusor*	*Emydura*	*Pseudemydura*
21	A1 seam contact (see Fig. 1)	absent	absent	present	absent	absent	absent
22	C6 seam contact (see Fig. 1)	absent	absent	present	absent	absent	absent
23	Interhumeral contact	yes	yes	yes	yes	yes	no
24	Precentral (nuchal) scute	present >90%	absent	present >90%	present >90%	present >90%	present >90%
25	Neck tubercles	low blunt	long sharp	long sharp	long sharp	very low blunt	short sharp
26	Eye color	dark unpatterned	patterned	bright patterned	dark unpatterned	patterned	patterned
27	Nictitating membrane	absent	absent	absent	vestigial	absent	absent
28	Head shield	present	present	present	present	absent	present
29	Barbells	large	large	large	large	small	small
30	Pigment loss, adult head	yes	no	no	no	no	no
31	Rostral pores	rare	present	absent	absent	present	present
32	Cloacal bursa, lining (Legler and Georges, 1993)	fully simple papillose	partly simple papillose	fully branched papillose	partly simple papillose	partly simple papillose	partly simple papillose
33	Esophageal glands (Legler and Georges, 1993)	3-parted	3-parted	3-parted	3-parted	3-parted	7-parted
34	Karyology: 2n (Bull and Legler, 1980)	50	50	50	unknown	50	50
35	Karyology: morphology (Bull and Legler, 1980)	no acrocentric	no acrocentric	no acrocentric	unknown	no acrocentric	2 acrocentric
36	Adh	B or E or F	B or C	D	?	B or BC	?
37	Ak-1	A	B	A	A	A	?
38	Ak-2	A or AC	A	E	A	AE or E	?
39	Ca-2	B or C	C	C	C	C	?
40	Dia	B	B or C	B	B	D	?
41	Fum	B or BC	AB or B	B	B	B or BC	?
42	Glo-1	A	A	B	B	A	?
43	Hbdh	C or D	C or D	C	F	C or CF	?
44	Idh-1	C or E or F	B or E	D	E	B	?
45	Lap	B	B	B	C	AB or B	?
46	Mpi-1	A or B	D	B	B	D	?
47	Pep-A	A or B	A	A	A	B	?
48	6Pgd	CD or D	B or F	E	HI	CD or D	?
49	Pgm	C or D	A	C	C	AC or C	?
50	Sod	C or D	C or D	C	D	C or CD	?
51	Tpi	A or B	A	A	A	A	?

and the common ancestor of *E. dentata*, *E. latisternum*, and *Emydura* as an unresolved polytomy; *Emydura* and *Elseya dentata* were regarded as sister groups.

Although we now think of a less close relationship of the *Elseya* (*dentata*) and the *Elseya* (*latisternum*) genera, we are reluctant to regard either the distance analysis or the cladistic analysis as the end point in our thinking. We therefore treat the problem of shortneck relationships as unresolved pending the completion of work in progress by Legler.

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