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A NEW GENUS AND SPECIES OF CHELID TURTLE FROM QUEENSLAND, AUSTRALIA^{1,2}

By John M. Legler³ and John Cann⁴

ABSTRACT. The Fitzroy Tortoise, *Rheodytes leukops*, new genus and species (Family Chelidae), is described from a large series of adults and juveniles from the Fitzroy drainage of Queensland, Australia (type locality 23°09'S, 149°55'E). No previous mention of this taxon appears under any name in the scientific literature. Each of the following characteristics alone will distinguish *R. leukops* from all other chelids: interlateral seam contacts on posterior parts of marginals 6 and 8; rib tips of costals 2-4 forming gomphoses with centers of peripherals 4-6; splenial bone lacking. *Rheodytes leukops* occurs in microsympatry with *Elseya dentata* and *Emydura krefftii*. *Chelodina longicollis*, *C. expansa*, and *Elseya latisternum* occur nearby in the same drainage. *Rheodytes leukops* is completely carnivorous (feeding chiefly on aquatic insect larvae), occurs in fast, clear water, and seems to be specialized for bottom probing and scraping. Annual reproductive potential is 46-59 eggs in 3-5 clutches. The eggs are small and have a mean incubation time of 47 days at 30°C.

Rheodytes leukops is seemingly most closely related to the eastern Australian short-necked chelids (genera *Elseya* and *Emydura*), but the phylogeny of *Rheodytes* is not yet understood. The following related generic groups of short-necked Australian chelids are defined on the basis of shell and scute proportions, form, skull and shell osteology, integumentary topography, color, and reproductive and dietary habits: (1) *Rheodytes*; (2) *Elseya dentata* group; (3) *Elseya latisternum* group; and (4) *Emydura*. *Pseudemydura* constitutes the fifth short-necked genus and seems not to be closely related to any other group in Australia.

Cann received a moribund specimen of an unusual turtle from a reptile park in 1973; the specimen had been collected on the Fitzroy River "near Rockhampton" and is now cataloged as AM R41274. Another specimen (AM R41794) was received by the Australian Museum in April 1974. We examined these two specimens in July 1974 and quickly recognized them as a strikingly new and different taxon. Seemingly, no other specimens of the Fitzroy Tortoise were in existence at that time. We obtained the specimens upon which this account is based in October 1976. An illustrated popular account of this expedition and the specimens collected appeared in Cann (1978).

METHODS AND MATERIALS

Abbreviations used for museums are as follows: AM, Australian Museum, Sydney; LACM, Los Angeles County Museum of Natural History; NMV, National Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; UU, University of Utah, Salt Lake City; WAM, Western Australian Museum, Perth. Other frequently used abbreviations: CL, carapace length; CW, carapace width; CBL, condylobasilar length; M, marginal; P, peripheral.

Measurements of the shell and terminology of shell elements, unless specifically explained, are as outlined by Carr (1952). Lengths of plastral scutes are interlaminal (i.e., an average of right and left scutes as measured on their common midventral seam).

Skull measurements that are not self-evident from their terminology are: Condylobasilar Length—from posteriormost

point of occipital condyle to anteriormost point of premaxillary region; Squamosonasal Length—from a line joining posterior tips of squamosals to the anteriormost projection of the nasals; Height of Snout—from top of nasal bones to tomial edge of maxilla, in a line perpendicular to basicranial-palatal plane; Maxillary Breadth—width of skull across posteriormost edges of maxillary tomium; Length of Dentary Symphysis—measured with mandible oriented on a plane surface and parallel to that plane surface (i.e., not maximal); Greatest Length of Mandible—on midlongitudinal axis from line joining posteriormost points of rami to anterior tip of dentary symphysis; Greatest Width of Mandible—maximum outside breadth—the base of the mandibular triangle.

Tinkle (1962) demonstrated the utility of expressing the points at which the five interlateral seams of the carapace intersect the marginal scutes. The terminology used here is as fol-

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lows: P, contact on posterior half of marginal; M, contact at midpoint; A, contact on anterior half (this terminology is a simplification of that used by Tinkle).

The type locality and most of the other localities mentioned in this paper can be found on the following maps. Australia 1:250,000, Series R 502, Ed. 1-DNM: Duaringa SF 55-16; Rockhampton SF 56-13. World Aeronautical Chart ICAO 1:1,000,000: Rockhampton, 3235 5th Ed.; Operational Navigation Chart 1:1,000,000: ONC-Q15: ONC-P15; *The Reader's Digest Complete Atlas of Australia*, 1968, Reader's Digest Assn. Pty. Ltd. Sydney, 183 pp (ca. 1:1,265,000): Clermont, pp 84-85; Brisbane-Rockhampton, pp 60-61. All the aforementioned maps have longitude and latitude and permit precise reckoning of localities. The Reader's Digest Atlas and the 1:1,000,000 aeronautical sheets are especially recommended. Coverage of the latter is worldwide.

SYSTEMATICS

Rheodytes, NEW GENUS

Figures 1 through 7

TYPE SPECIES. *Rheodytes leukops*, new species, by monotypy.

VERNACULAR NAME. Fitzroy Tortoise.

DIAGNOSIS. A short-necked Australian chelid distinguished from all other members of the Chelidae by the following characters (each character marked with an asterisk (*) is alone diagnostic among chelids): (1)* interlateral seam contacts on the posterior parts of the sixth and eighth marginal scutes; (2)* rib tips of costals 2-4 forming gomphoses with the centers of peripherals 4-6; (3) a narrow, unridged maxillary triturating surface that becomes even narrower in the premaxillary region; (4)* splenial bone lacking; (5) a long completely coossified dentary symphysis; (6) a maxillary tomial edge that is straight in profile; (7) a white ring around the iris; (8) relatively small eggs and short incubation period; (9) huge cloacal bursae.

ETYMOLOGY. The generic name is derived from the Greek roots *rheos* (current or stream) and *dytes* (diver) and alludes to the speed and agility of these animals in fast currents. The specific name is derived from the Greek *leukos* (white) and *ops* (eye) and refers to the distinctive white ring around the iris.

RELATIONSHIPS. Superficially similar to and probably most closely related to the genera *Emydura* and *Elseya* but distinguished from them by the above phenotypic characters (in combination or by each of the first four diagnostic characters alone). Of these, *Elseya dentata* seems most closely to resemble *R. leukops* (Table 1). *Rheodytes leukops* occurs microsympatrically with *Elseya dentata* and *Emydura krefftii*.

Rheodytes leukops, NEW SPECIES

Figures 1 through 7

HOLOTYPE. QM J31701, whole adult female with carapace length of 253 mm, collected 7-8 October 1976 by J.M. Legler and J. Cann: Fitzroy River, 63 km N and 25 km E of Duaringa, Queensland, Australia, elevation 40 m (23°09'S, 149°55'E). Bearing also the numbered tags "UU Field JML 8217" and "UU 17111" (Fig. 1, Table 2).

ALLOTYPE. QM J31702, whole adult male with carapace

length of 235 mm, same data as holotype (JML 8215 and UU 17109).

PARATOPOTYPES. LACM 127779, UU 17131, AM R44651, whole adult males; UU 17103 male skeleton; UU 17104-7 males, dry shell with soft parts and viscera in liquid (hereinafter "S & P" specimens); LACM 127778, UU 17110, 17113, 17122, AM R44650, whole adult females; UU 17114-5 female skeletons; UU 17116-21 females, S & P specimens. UU 16805-820, 17150-86, 17197-226, QM J31704-7, AM R44652, hatchlings representing six clutches of eggs from paratopotypic females.

OTHER PARATYPES. Fitzroy River, Glenroy Crossing, 60 km N and 23.5 km E of Duaringa, Queensland, elevation 40 m (23°11'S, 149°56'E), 9 October 1976, Legler and Cann: UU 17124-6 females, S & P specimens. UU 17132-49, 17227-45, LACM 127780, NMV 50435, UU 17248-66, hatchlings representing three clutches of eggs from paratypic females. Dawson River, 2 km N of Gainesford, Queensland, elevation 64 m (23°47'S, 149°46'E), 10 October 1976, Legler and Cann: UU 17127 male, 17128 female, QM J31703 female, all prepared as S & P specimens. Windah Creek, near Gogango, Queensland, elevation 80 m (23°37'S, 150°02'E), 15 September 1976, AM R44650 whole adult female. "Mackenzie River, Dawson Valley, Queensland" 3 April 1974, R. Stokes: AM R41794 whole adult male. "Fitzroy River, Queensland" November 1973, R. Ohl: AM R41274 whole adult female.

DIAGNOSIS. See diagnosis of genus *Rheodytes*.

GENERAL DESCRIPTION OF SPECIES (based on hypodigm). Dorsal silhouette of adult carapace a tapered ellipse lacking any distinct, straight, lateral edge. Widest point at M7 or M7-8. Juvenile carapace nearly round. Plastron never visible in dorsal view of either whole animal or dry shell (Figs. 1, 5, and 7).

Edge of carapace smooth in adults, extremely serrate in juveniles up to 95 mm long and 2-½ years old (older juvenile stages unknown at this writing); serrations consist of single projections on individual marginal scutes as follows: M1 unmodified; M2-4 slightly pointed; M4-6 sharply pointed with spines directed posteriorly; spines on individual marginals 7 through 12 become progressively broad and blunt (Fig. 3).

Optical cross section low (Table 3 and Fig. 5) either peaked or slightly flattened middorsally; marginal index (vertical height of margin expressed as a percentage of total height), 0.45.

Plastral lobes relatively narrow, tapered, and straight-sided. Forelobe foreshortened and tapered to a blunt point (rather than truncated). Anal notch semicircular, never angular (Figs. 1 and 7).

Head narrow and high. Orbits small and (because of narrow rostrum and interorbital region) appear to be directed more anteriorly than in other short-necked chelids. Maximum breadth of head at midposterior border of tympanum (at quadrato-squamosal suture); optical cross section of head suggests a high rectangle with sides angled slightly inward dorsally. In profile, there is a continuous even slope formed by dorsum of rostrum and head (no supraorbital or rostral bulges). In general, the head appears relatively small and the neck relatively large, the combination suggesting a powerful instrument for digging or prying (Figs. 3, 4, and 6).

Posterior edge of maxillary sheath (near angulis oris) forms angle of about 45 degrees with main axis of maxillary tomial

edge. From that angle to premaxillary region, the tomial edge is almost perfectly straight in profile (no concavity, no convexity). In anterior view, the sheath is flat or slightly concave in premaxillary region. Maxillary tomial edge lacking distinct notches or denticulation of any sort. Tomial edge of mandibular sheath concave in profile, gently curved from angulus oris to tip; tip bluntly rounded, neither a hook nor a crushing device. In general, the tomial edges of the jaw sheaths appear to be worn in adults; in the largest adults, the anterior parts of the tomial apparatus barely occlude.

Precentral scute present in 27 (93 percent) adults. Modal carapacial seam contacts 2M 5A 6P 8P 11A (see "Methods and Materials"). Modal formula for three longest scutes on plastron Fem > An > Ab. Length of femoral scute approximately 20 percent of carapace length (Table 3). A slight plastral concavity along midline in adults of both sexes.

Epidermal laminae relatively thin. Intercostal sutures visible through lateral scutes in adults except in most heavily pigmented specimens. Plastral and interperipheral sutures easily discernible through scutes. Epidermal laminae thickened and weltlike over interosseous sutures.

Surface texture of carapace (under low magnification) consisting of a primary series of sharp parallel ridges (longitudinal or diagonal, depending on scute) separated by narrow sulci;

smaller secondary cross ridges create a series of pits that appears as a reticulation to the unaided eye. Plastron smooth, lacking a distinctive texture. Growth zones weakly evident in captive-reared juveniles but not at all evident in adults.

Feet and hands large and fully webbed. Claws 5-4. An extensive ulnar fringe of enlarged scales on foreleg. Tibial edge of leg lacking a distinct series of enlarged scales (Figs. 3 and 4). Two musk gland orifices—one below posterior part of M3 and one below anterior part of M7.

Triturating surfaces of maxillary sheath relatively narrow and at right angles to plane of tomial edge, about as wide as tomial edge is deep. A slight expansion in width of triturating surface just anterior to internal nares at which point the sheath is about 1 mm thick. From that point anteriorly, triturating surface narrows quickly and significantly to about 25 percent of its narrowest posterior width. The "U" formed by the two triturating rami anteriorly bounds a thick pad of buccal mucosa that covers nearly the entire premaxillary region of the palate. This anterior extension of palatal mucosa is rounded and tumescent-appearing in live specimens but is dented or collapsed in most preserved specimens. The tumescence consists of a thick (16 to 20 cell layers) pad of nonkeratinized epithelium underlain by loose connective tissue and a large vascular sinus.

Choanal papillae lacking; mucosa of buccal and pharyngeal

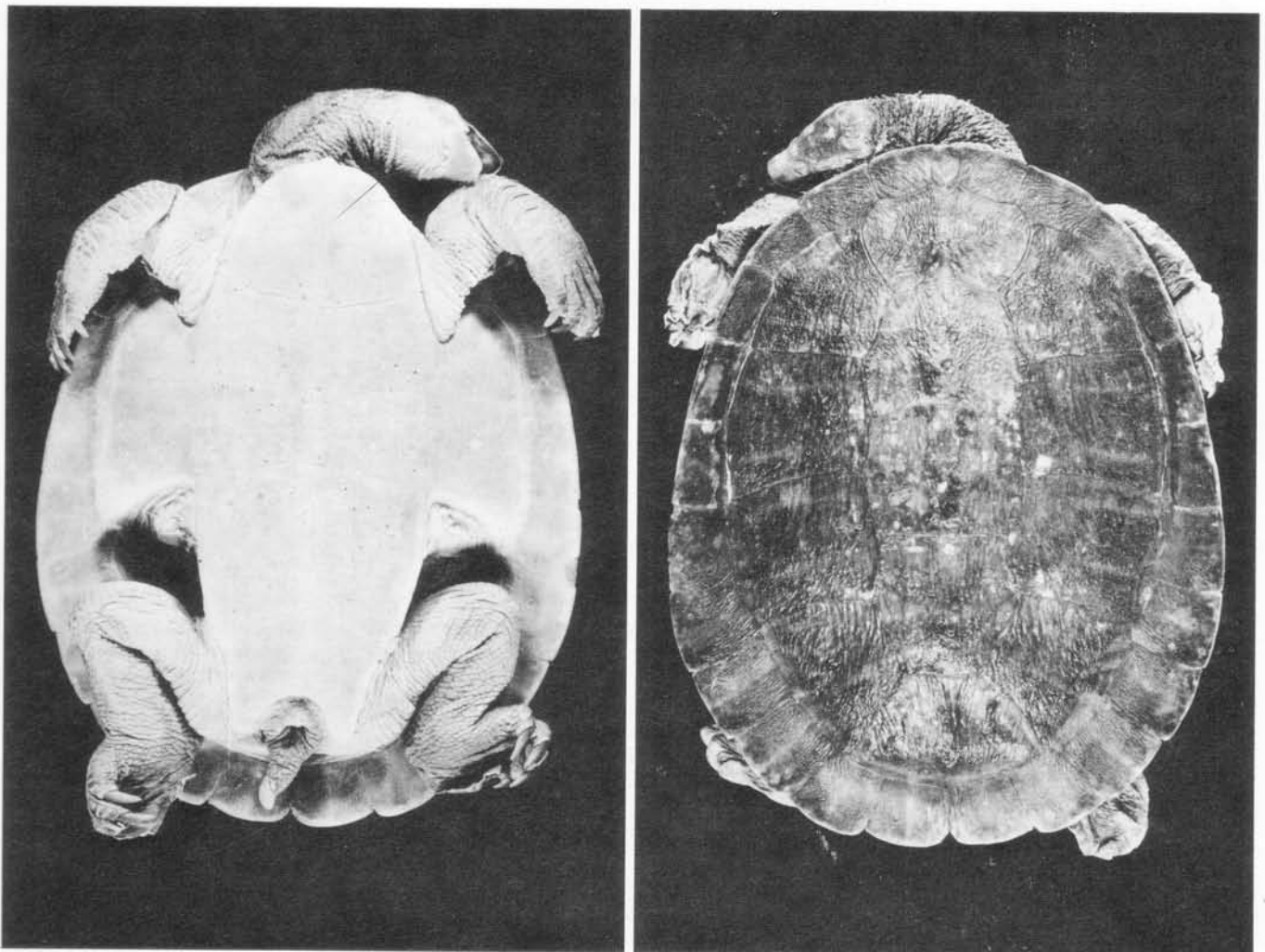


Figure 1. *Rheodytes leukops*, new genus and species: Holotype QM J31701, adult ♀, carapace length, 253 mm.

Table 1. Comparison of selected characters in four major groups of Australian short-necked chelids, excluding *Pseudemydura* (see also "Discussion"). Remarks under *Emydura krefftii* apply to all known members of the genus in Australia and New Guinea.

<i>Rheodytes leukops</i>	<i>Elseya dentata</i>	<i>Elseya latisternum</i>	<i>Emydura krefftii</i>
Cross section relatively low, slightly peaked, relatively steep-sided; marginal index, 0.45 (see description).	Cross section evenly rounded from margin to margin, never peaked or depressed mid-dorsally; marginal index, 0.44	Cross section evenly rounded from margin to margin; often flat-topped or with a midlongitudinal depression; marginal index, 0.53	Cross section rounded above (never peaked or depressed) and steep-sided; marginal index, 0.40
Anterior lobe of plastron not extending anterior to edge of carapace, not visible in dorsal view.	Anterior lobe of plastron with anterior projection to or beyond anterior edge of carapace, usually visible in dorsal view.	Anterior lobe of plastron not extending anterior to edge of carapace, not visible in dorsal view.	
Lateral and posterior marginal serration extreme in hatchlings but completely lost in adults.		Marginal serration moderate to extreme posteriorly in young and adults.	No marginal serration at any stage.
Precentral scute usually present (93%).	Precentral scute usually absent (94%).	Precentral scute geographically variable; usually absent in far northern populations (Cape York, 93%) usually present and well developed in populations south of 29°S (98%).	Precentral scute usually present (99%).
Interlateral seams (C and D after classification of Tinkle 1962) contacting posterior parts of marginals 6 and 8 (Fig. 7).	Interlateral seams C and D forming contacts with marginals 7 and 9, usually medially or anteriorly, contacts with M6 and M8 occurring only rarely or as anomalies.		
Modal plastral formula Femoral > Pectoral > Anal (41%); Femoral always longest (100%).	Modal plastral formula Femoral > Pectoral > Abdominal (50%); Femoral (79%) or Pectoral (21%) longest.	Modal plastral formula Anal > Pectoral > Intergular (24%); Anal (73%), Femoral (10%), or Pectoral (10%) longest.	Modal plastral formula Pectoral > Femoral > Abdominal (48%); Pectoral (78%) or Femoral (21%) longest.
Maxillary tomial edge nearly straight in profile from premaxillary region to posterior end (not curved, not indented) where it forms a 45° angle with straight posterior edge of sheath extending to angulus oris.	Maxillary tomial edge curved in profile from premaxillary region to angulus oris (a "smile"); premaxillary region depressed at least slightly.		
No median alveolar ridge.	A well defined median ridge on alveolar surfaces of maxilla and dentary, evident on both osseous and keratinous parts of jaw apparatus (evident in all populations of <i>E. dentata</i> but less well developed in northwestern Australian <i>E. dentata</i> and in <i>E. novaeguineae</i>).	No median alveolar ridge.	No median alveolar ridge.
Diet carnivorous, insectivorous; no known malacophagous tendencies.	Diet herbivorous (Legler 1976).	Diet chiefly carnivorous with insectivorous tendencies (vegetation rare in guts examined); no malacophagous tendencies.	Diet omnivorous, opportunistic, geographically variable; aquatic vegetation common in guts; malacophagous modifications in several populations.
Always one pair of distinct, conical, small to medium barbels; little variation.	One, two, or three barbels; often a single median barbel in northwestern Australian populations; a tendency toward thick, fleshy, variable barbels.	Number of barbels variable but usually two in a balanced pair, never single and median; usually well developed and tending to be long.	Barbels poorly developed or absent, rounded tubercles at most; seldom conical, never single and median; often indistinguishable from other scales on skin.
No rostral pores.	Rostral pores rare.	Rostral pores evident and well developed (Winokur and Legler 1974).	
Head shield fully keratinized and extensive at all ages; gnarled in older individuals.			Head shield usually absent; weakly developed only in largest adults (usually females); never gnarled.

Continued

Table 1 continued

<i>Rheodytes leukops</i>	<i>Elseya dentata</i>	<i>Elseya latisternum</i>	<i>Emydura krefftii</i>
Inguinal buttress nearly as broad transversely as axillary buttress; posterior part of sternal cavity almost as commodious as anterior part.	Inguinal buttress much narrower than axillary buttress in transverse section. Posterior part of sternal cavity much less commodious than anterior part.		
Rib tips of costals 2 through 4 articulate with gomphoses formed in the centers of peripherals 4 through 6, respectively.	Rib tips of costals 2 to 4 form articulations with the interperipheral sutures.		
Dentary symphysis coossified in adults, never visible.	Dentary symphysis an unmodified suture in most adults; coossified (but still visible) in a few large individuals.	Dentary symphysis coossified in adults; never visible.	
Splenic bone lacking, probably fused with prearticular.	Splenic bone present as a distinct separate element of lower jaw.		
A well-developed retroarticular process on mandible.	Mandibular retroarticular process small or lacking.		
Ventral processes of prefrontals closely approximated at midpoint of <i>fissura ethmoidalis</i> to create keyholelike aperture in <i>fossa nasalis</i> .	Ventral processes of prefrontals not closely approximated, not constricted, permitting virtually unobstructed view posteriorly through <i>fissura ethmoidalis</i> .		
Ventral ridges of frontal bones vertical, not turned inward, not closely approximated.	Ventral ridges of frontal bones turned sharply inward and closely approximated, nearly closing <i>sulcus olfactorius</i> at midpoint.	Ventral ridges of frontals as in <i>R. leukops</i> .	
Prefrontals narrowly exposed dorsally, forming only a small part of dorsal orbital rim.	Prefrontals broadly exposed on anterior part of dorsal orbital rim.		
At least a narrow maxillary-frontal contact preventing prefrontal-nasal contact on dorsal exposure of skull.	Prefrontals and nasals in contact, excluding a maxillary-frontal contact on dorsal exposure of skull.		
Iris ivory in adults, silvery in young.	Iris dark (brown to black) even in young specimens.	Iris pale, usually yellowish, never ivory, silver or dark.	

roof more or less smooth. Tongue fleshy, unspecialized, bearing transverse or oblique folds that are devoid of complex, macroscopically visible papillae. Nictitating membrane lacking; lower eyelid semitransparent (juvenile) to translucent (adult), permitting view of eye even when closed.

One pair of distinct uniformly pale barbels; in form of flattened cones with rounded tips, basal diameter 60 to 80 percent of length. Other slightly pointed tubercular scales (quite distinct from the barbels) along medial edge of each mandibular ramus just behind barbels. Barbels tend to point slightly forward in living specimens (Figs. 3, 4, and 6). Surface topography of barbels (under magnification) consists of shallow anastomosing grooves on distal half and a series of juxtaposed scalelike structures on basal half.

No sign of rostral pores (Winokur and Legler 1974) in any specimen examined; soft skin of snout absolutely smooth between natural boundaries of maxillary sheath and rostral extension of head shield.

Entire epidermis pitted in adults, degree of pitting seemingly

directly correlated with age; cause of pitting unknown but probably pathologic; most evident on head shield and plastron; reflected secondarily on underlying dermal bone.

Large pointed conical tubercles on dorsum of neck, a few of which may have flattened apices but none of which were found to have specialized follicular centers (Legler and Winokur 1979). Each tubercle set on a small hillock, which bears also a number of smaller granular scales; the larger the neck tubercle, the larger the hillock. Rows of large tubercles seemingly transverse in nape region and longitudinal elsewhere—five discernible rows on posterior part of neck, seven in region of nape. Neck tubercles of adults upright in most cases; those of juveniles in shape of flattened triangles or flattened cones, depressed, soft, and lying down upon the skin—not rigid and upright as in adults.

Ventral surface of neck bearing a series of very low conical or hemispherical tubercles, each on a hillock that is surrounded by many very low granular scales. Granular scales have a rough feel, which is probably imparted by micropustules.

In juveniles, the primary topography of the neck skin seems to be that of rather low plaquelike juxtaposed scales, which are in turn covered with discernible (under low magnification) micropustules. The shape of the scales and their pustulate secondary topography gives the skin the appearance of crystallized sugar. This is less distinct in specialized areas such as the dorsal

neck, where tubercles occur, but the tubercles regardless of size also have the micropustulate secondary topography.

Head shield well developed and fully keratinized, smooth to slightly pitted and rugose in females, extremely gnarled in older males. Head shield extends posteriorly from rostrum (anterior edges of nasal bones) and corresponds thence to the gen-

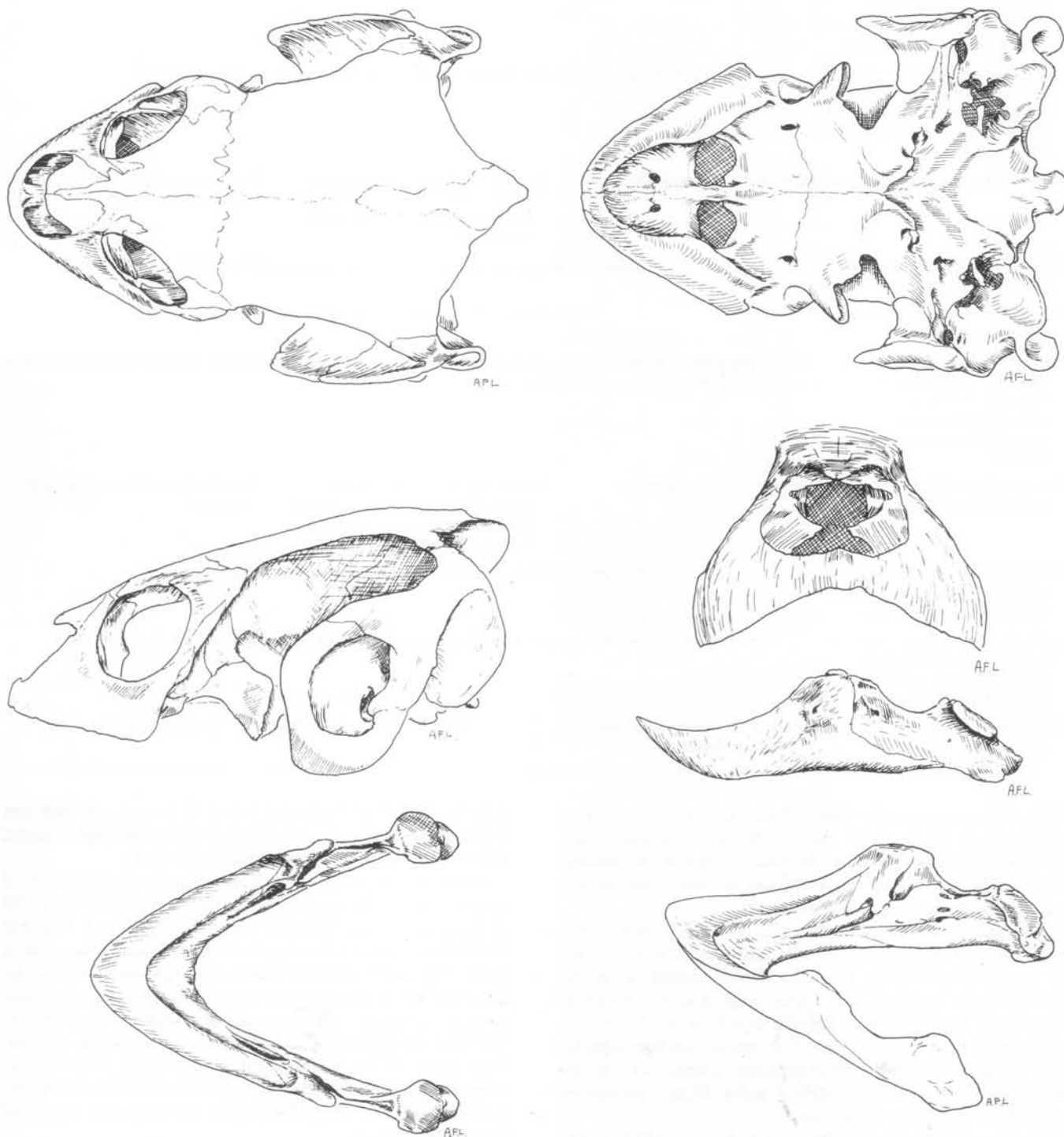


Figure 2. *Rheodytes leukops*, new genus and species: Paratype UU 17114♀, condylobasilar length 41.6 mm; three views of entire cranium, three views of mandible, and a view directly into the narial aperture (note keyhole-shaped *fissura ethmoidalis* formed by descending processes of prefrontal bones).

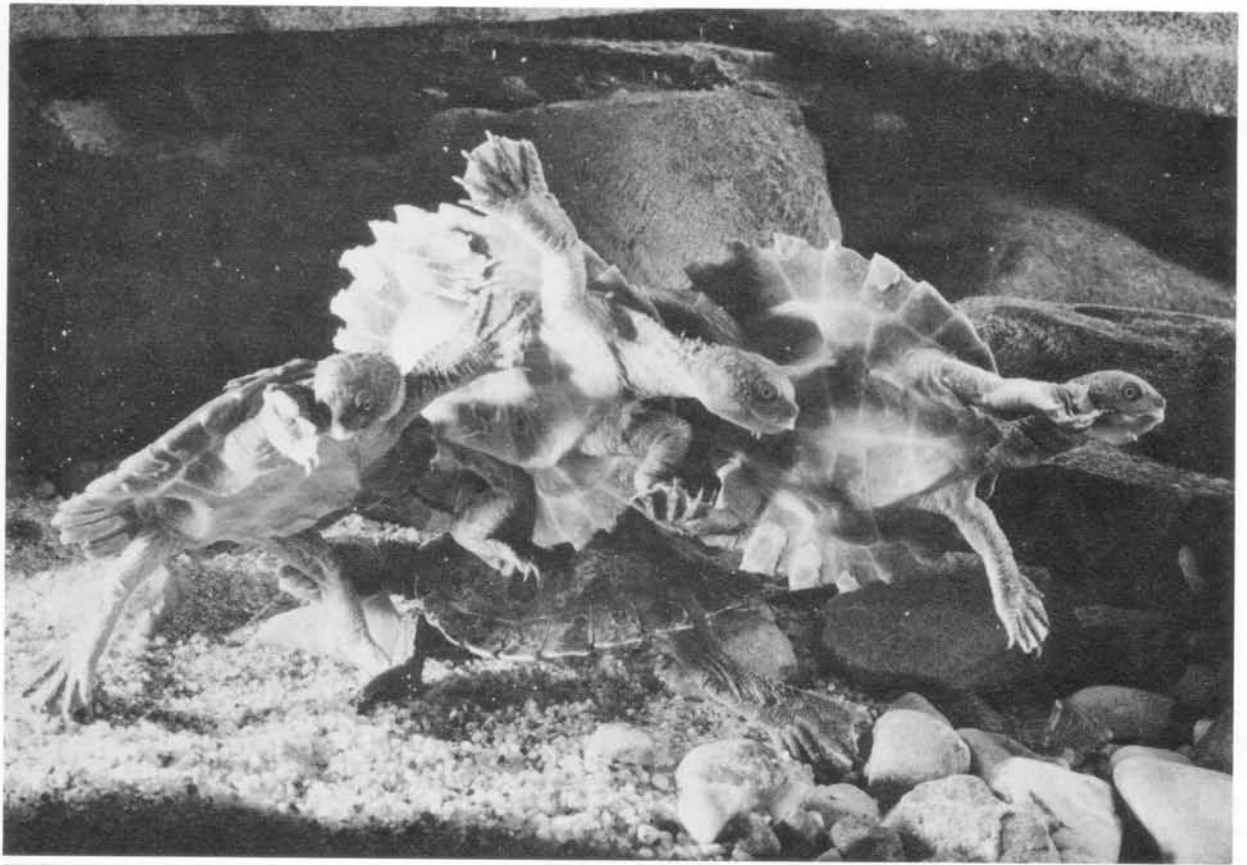


Figure 3. *Rheodytes leukops* juveniles approximately 16 months old and 60 mm carapace length (UU 17219-22). Top: Three juveniles swimming rapidly apart after clinging together in a tight group; one individual is inconspicuous at bottom; note shell serration and relative proportions of juveniles. Bottom: Three of above individuals in gregarious clinging postures; note development of mandibular symphysis.

Table 2. Selected measurements (in mm) of the holotype (QM J31701♀) and nine topotypic paratypes of *Rheodytes leukops*, new genus and species. Widths of plastral forelobe and hindlobe were measured at humeropectoral seam and at midfemoral scute, respectively.

Collection and Catalog No.	Carapace Length	Carapace Width	Plastron Length	Plastral Forelobe Width	Plastral Hindlobe Width	Shell Height	Head Width
Females							
UU 17110	257	201	211	75	81	88	33
QM J31701	253	203	205	73	80	70	31
UU 17112	245	204	208	73	76	80	33
UU 17113	241	187	198	72	73	73	31
UU 17114	253	198	216	71	78	78	33
Mean	249.8	198.6	207.6	72.8	77.6	77.8	32.2
Males							
UU 17104	251	200	208	69	77	72	36
UU 17105	262	207	212	72	80	76	38
UU 17106	246	200	198	68	77	78	37
UU 17107	238	188	195	63	70	77	38
QM J31702	235	195	188	67	71	64	33
Mean	246.4	198.0	200.2	67.8	75.0	73.4	36.4

eral dorsal exposure of dermal skull roofing elements, closely following free upper edge of orbit, having a slight ventral extension at origin of postorbital bar, corresponding to lateral edges of parietals, and ending more or less evenly with the posterior edges of parietals. A slight posteroventral extension along post-temporal bar. Occasionally a blunt extension near base of supraoccipital spine. Posterior edge of head shield usually broken up partly or completely into scalelike divisions. In general, all extensions, ridges, and other surface topography of head shield are intensified in older males to produce an overall gnarled appearance. Anterior vertical extension of maxillary shield (extending between eye and snout) also higher in old males than in females (Fig. 6).

In profile, tympanum and head shield delimit a distinct region, in the shape of an inverted parenthesis, beginning at angulus oris and extending to posterior temporal region—about 8 mm wide. This is an area of soft skin in which there are rather widely spread low, pointed, conical tubercles or very low rounded tubercles, with a few soft longitudinal ridges. Tympanum covered by a series of soft longitudinal skin ridges, none of which is ossified. Tympanum bordered by tubercular scales but lacking such scales on its surface. Large scales of temporal region separated by smaller granular scales and small longitudinal ridges.

KARYOTYPE. One juvenile was karyotyped (see Bull and Legler, 1980, for account of karyotypic relationships in pleurodires). Diploid number 50; fundamental number 72; 11 pairs of biarmed macrochromosomes of which the first three are metacentric, submetacentric, and subtelocentric, respectively. The remaining 14 pairs are microchromosomes. The karyotype is virtually indistinguishable from those of other short-necked Australian chelids.

OSTEOLOGY. The following account is based on 3 complete and 16 partial skeletons (lacking skull). Phalangeal formula 2-3-3-3-3 on hand and foot. Cervical central articulations typically chelid (Williams 1950)—5 and 8 biconvex, 7 amphicoelous, 6 procoelous, the others opisthocelous. Sclerotic ossicles 13.

Shell thin and in general lightly built. Plastron typically chelid, having four pairs of osseous elements plus an ento-

plastron. Hyo- and hypoplastral bones greatly thickened along median interosseous sutures, the anteroposterior extent of the thickening corresponding almost perfectly to anteroposterior limits of bridge. Inguinal buttresses almost as broad transversely as axillary buttresses; posterior part of sternal cavity almost as deep (commodious) as anterior part. Neural bones lacking. Rib tips of costals 2-4 forming gomphotic articulations in the centers of peripherals 4-6, respectively (not in the inter-peripheral sutures; Fig. 7).

Carapacoplastral articulation sutural but containing enough soft connective tissue to permit some kinesis. Dried shells prepared in caustic solutions show considerable gaps between carapace and buttresses.

Skull definitely prognathous in profile (Figs. 2, 4, and 6) due to anterior projection and overhang of premaxillary region; supraoccipital process relatively short; trigeminal foramen not visible in lateral view. In dorsal aspect, maxillary bone contacts frontal and separates prefrontal from nasal; prefrontals very narrowly exposed dorsally, forming only a small anterior part of dorsal orbital rim. Ventral ridges on frontal bones (forming *sulcus olfactorius* [Gaffney 1972]) straight, not turned inward, not closely approximated. Descending processes of prefrontals having transverse plates forming posterior wall to nasal cavity and bounding a keyhole-shaped *fissura ethmoidalis* (Gaffney 1972). Occipital region of skull bearing massive facets for attachment of nuchal muscles (see Shah 1963) as follows: deep facets on posterior faces of squamosal and opisthotic bones; a large concave facet and four heavily developed posterior processes on ventral surface of basioccipital (Fig. 2).

Internal nares large. Anteriormost part of palate thin and forming a distinct semicircular depression bounded anteriorly and laterally by low ridges for attachment of maxillary sheath. Prepalatine foramina bordered by premaxillaries anteromedially and by maxillaries posterolaterally. Palate and maxillary region relatively narrow. Base of skull especially narrow at pterygoid "waist" just posterior to trochlear processes of pterygoids.

Mandibular ramus straight and lightly built; in dorsal aspect, lines drawn from tip of symphysis to centers of articular facets lie almost entirely within the ramus (and form a mean

angle of 46.5 degrees; Table 4). Intermandibular articulation long and coossified without trace of suture or symphysis. Splenial bone absent as individual bone in lower jaw. Meckelian canal and fossa broadly exposed below coronoid on medial face of mandibular ramus; coronoid-prearticular contact lacking in two specimens, a narrow contact in one specimen. Angular long, extending well past anterior extent of coronoid; tip of coronoid (1.5 mm) clearly visible in lateral view. Mandible bearing well developed retroarticular processes formed chiefly by the angular bones.

COLOR IN LIFE. The following color description is based on live, fresh-caught material. Adults were examined indoors in diffuse summer daylight. All parts described were viewed when slightly moist (after wiping with a damp cloth). Descriptions of hatchlings are based on numerous close observations in an aquarium lighted by a fluorescent bulb (Vita light). See Cann (1978) for color photos.

ADULT FEMALES (UU 17110, 17113, QM J31701, LACM 127778). Overall ground color of carapace medium to dark brown with a suggestion of olive in palest specimens; carapace dull (probably due to complex surface texture); slightly paler over interosseous sutures; no regular markings on carapace; a few specimens showing one to three small (5 to 15 mm diam.) elliptical black spots irregularly placed on carapace. Plastron unicolored in general aspect, ground color dark neutral straw to horn, somewhat darker near bridges; no distinct dark markings; no distinct darkening of interlaminal seams; areas where interosseous sutures are clearly visible through

scutes are suffused with pink; inframarginal surfaces slightly darker than ventral plane of plastron, interperipheral sutures showing through as distinct pale lines. Soft parts (other than head) generally pale to medium slatey olive-grey, not at all bright or distinctive. Interdigital webbing paler than rest of foot; enlarged scales on fore and hind limbs darker than ground color; ventral surface of thigh paler than dorsal surface—a slightly brighter pale ground color than plastron; skin of inguinal pocket dull yellowish cream. Dorsal aspect of head and neck uniform brownish (same shade as carapace), olive in palest specimens; ventral ground color pale yellowish-orange, the division between dark and pale colors along a line extending posteriorly from angulis oris; orange color intensified in a vertical bar on anterior edge of tympanum and just posterior to mandibular symphysis where it is nearly pink; barbels paler at tips than bases. Jaw sheaths pale neutral olive where underlain by bone, straw at free edges; maxillary sheath streaked with slatey gray; mandibular sheath uniform. Iris a narrow ivory-colored band surrounded by rich brown. Tongue and inside of mouth pale salmon pink.

HATCHLINGS (approximately 150 from 9 clutches). Carapace tan to pale brown; marked with blackish-brown flecks; each lateral and central scute bearing a keel on which there is an intensification of dark color; this results in a series of five vague black dots along middorsal line and four such dots on each side; dots not necessarily more evident than general flecking. Plastral ground color pale neutral slate; yellowish suffusion produced by translucency of plastron and underlying yolk mass;

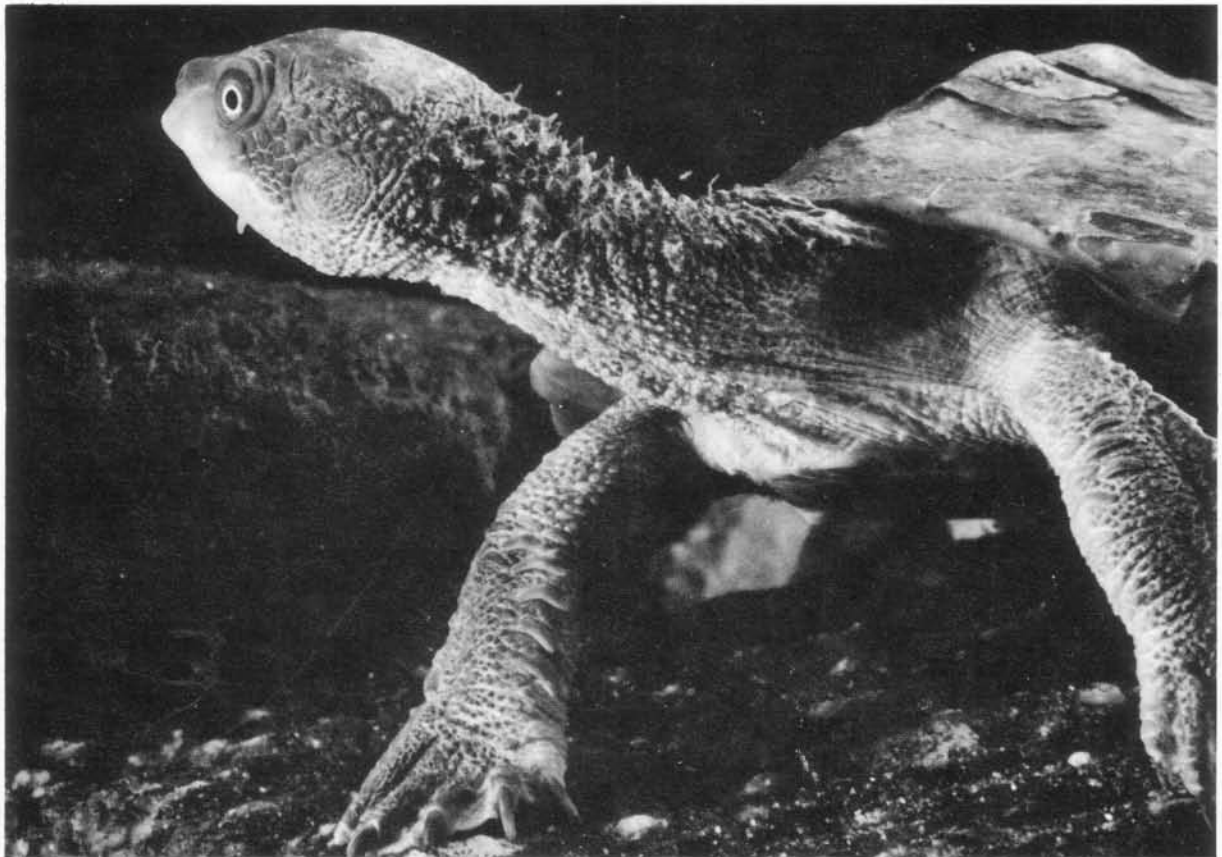


Figure 4. *Rheodytes leukops*, one of the individuals shown in Figure 3; note heavy development of neck and limbs and prognathous appearance of head.

Table 3. Comparisons of scute, head, and shell proportions for adults of four species of short-necked chelids (means and extremes for each sex). All specimens are from the Burnett, Fitzroy, and Raglan Creek drainage systems (latitudinal range 23°11' to 26°19'S). Note average size of adults (*E. dentata* largest, *E. latisternum* smallest) and degree of sexual dimorphism in size (least in *R. leukops*).

	Carapace Length (mm)	Head Width + CL	Least Inter- orbital Breadth + Head Width	Greatest Diameter of Orbit + Length of Mandibular Symphysis	Carapace Width + CL	Shell Height + CL	Femoral Scute Length + CL	Anal Scute Length + CL
<i>Rheodytes leukops</i>								
Males, N = 9	243 235-262	0.15 0.13-0.16	0.20 0.18-0.21	0.73 0.55-1.02	0.81 0.79-0.83	0.29 0.27-0.30	0.21 0.20-0.22	0.12 0.11-0.13
Females, N = 19	249 231-259	0.13 0.12-0.14	0.19 0.17-0.21	0.82 0.75-1.02	0.80 0.76-0.85	0.31 0.30-0.34	0.22 0.19-0.24	0.12 0.11-0.14
<i>Elseya dentata</i>								
Males, N = 9	263 249-269	0.17 0.15-0.19	0.27 0.24-0.29	0.91 0.81-1.17	0.79 0.77-0.85	0.33 0.31-0.36	0.22 0.19-0.23	0.10 0.09-0.12
Females, N = 9	343 309-374	0.17 0.15-0.19	0.26 0.23-0.30	0.85 0.64-0.99	0.79 0.75-0.83	0.35 0.31-0.40	0.21 0.18-0.24	0.10 0.09-0.12
<i>Elseya latisternum</i>								
Males, N = 6	164 148-172	0.19	0.24 0.22-0.26	0.97 0.91-1.09	0.80 0.79-0.83	0.30 0.29-0.31	0.15 0.13-0.17	0.18 0.17-0.19
Females, N = 3	232 172-271	0.20 0.20-0.21	0.24 0.23-0.26	0.80 0.70-0.98	0.80 0.78-0.81	0.31 0.30-0.32	0.14 0.13-0.15	0.18 0.16-0.19
<i>Emydura krefftii</i>								
Males, N = 10	221 187-256	0.15 0.13-0.17	0.25 0.22-0.28	0.90 0.75-1.07	0.73 0.75-0.79	0.36 0.34-0.38	0.19 0.17-0.21	0.11 0.10-0.13
Females, N = 16	272 234-277	0.17 0.15-0.19	0.26 0.22-0.30	0.73 0.59-0.95	0.76 0.71-0.82	0.38 0.36-0.41	0.18 0.15-0.20	0.12 0.09-0.13

Table 4. Skull proportions in adults of four species of short-necked chelids from eastern Australia. Means and extremes are given for each sex. See "Methods and Materials" for explanation of measurements.

	Condyl- basilar Length (mm)	Squamoso- nasal Length + CBL	Height of Snout + CBL	Mandible: Greatest Width + Greatest Length	Length of Dentary Symphysis + Greatest Width of Mandible	Maxillary Breadth + CBL	Mandibular Angle (degrees)
<i>Rheodytes leukops</i>							
Males, N = 1	40.0	0.94	0.16	0.85	0.33	0.49	46.3
Females, N = 2	42.3 41.6-42.9	0.92 0.91-0.94	0.15 0.13-0.17	0.85 0.84-0.87	0.35 0.34-0.35	0.50	46.4 46.3-47.0
<i>Elseya dentata</i> (Burnett and N. Johnstone drainages)							
Males, N = 2	49.3 48.5-50.1	1.05 1.01-1.08	0.19 0.16-0.21	0.95	0.24 0.23-0.25	0.53 0.52-0.55	51.0 50.9-51.1
Females, N = 3	63.9 56.7-69.0	1.03 1.03-1.07	0.20 0.20-0.21	0.96 0.90-1.03	0.26 0.21-0.32	0.54 0.53-0.55	51.2 48.8-54.2
<i>Elseya latisternum</i> (Cape York Peninsula)							
Males, N = 2	40.3 38.9-41.8	0.98 0.95-1.01	0.22 0.21-0.23	0.95 0.95-0.96	0.28 0.27-0.29	0.57 0.55-0.59	51.1 50.8-51.3
Females, N = 4	48.4 46.6-49.2	1.01 0.99-1.03	0.21 0.20-0.22	0.95 0.92-0.98	0.31 0.29-0.32	0.59 0.57-0.61	50.9 49.7-52.3
<i>Emydura krefftii</i> (Burdekin drainage)							
Males, N = 3	39.3 39.0-39.4	0.99 0.97-1.02	0.21 0.19-0.23	0.90 0.86-0.93	0.25 0.23-0.27	0.54 0.53-0.55	48.8 46.5-49.7
Females, N = 4	43.9 41.5-46.5	0.99 0.98-0.99	0.19 0.18-0.19	0.95 0.91-0.98	0.27 0.26-0.27	0.59 0.57-0.61	50.7 49.0-52.5

irregularly flecked with melanin, flecks tending to be concentrated on anterior lobe and bridge (posterior lobe immaculate in some individuals). Iris a metallic silvery-blue, not the clear ivory of adults. Hatchlings placed under water on fine brownish river sand were well camouflaged.

ONTOGENETIC COLOR CHANGE. There seems to be a gradual paling of colors in females as they grow older, but this is not at all distinct. There is a rather distinct change that occurs in males with age, culminating in a series of bright contrasting colors on the head and neck. This seems to be a process of progressive melanin loss and its replacement by orangish-yellow or rosy pigment in some areas. In general, these areas are the upper eyelids, the region around the tympanum, and to a lesser extent, the snout and throat. The oldest and brightest males we have examined (not necessarily the largest) present a rather handsome, striking, tricolored appearance with an immaculate greenish-olive maxillary sheath, an orange-ringed eye, and to a lesser extent, an orange-ringed tympanum (giving the animal a clown-faced appearance; Fig. 6). Although the color of the iris does not change in older males, it is set in a more contrasting situation (the pale iris, the surrounding dark part of the eyeball, the surrounding orange ring on the eyelids, and the very dark brown ground color).

ECOLOGY

HABITAT. In the region of the type locality, the Fitzroy River flows northwestward; large deep pools alternate with fast shallow riffles. The type locality is a riffle 15 to 27 m wide and 400 m long, grading from a depth of 0.3 to 0.6 m at its upstream limit (where the stream is fordable) to 2.5 to 3.0 m at its downstream limit (Fig. 8). Above the riffle, there is a pool about 1 km long with high, earthen, wooded banks. The riffle flows into a similar downstream pool, which is 2 to 3 km long. Current in the large pools is undetectable, and depths are in excess of 10 m; the bottom is rocky, with a heavy layer of silt, especially near the banks. Current in the riffle varies from very fast at the upper end (difficult to wade without support) to slow at the downstream end (scarcely noticeable when diving).

A total of 35 adults of *Rheodytes leukops* was obtained; 28 of these were retained for study, and 7 were released at point of capture. Most of the specimens were captured by diving with a face mask and snorkel (one was caught in a gill net). We therefore had the opportunity to observe all resident turtle species under water. We dived once in the lower part of the large upstream pool and repeatedly in the entire length of the riffle. Gill nets were set in the downstream pool, but we did not dive there because of the presence of large crocodiles (*Crocodylus porosus*, 3 to 3.6 m total length). Underwater visibility in the riffle was 1.2 to 2.4 m; water temperature was 25.5°C.

Rheodytes leukops definitely prefers fast water. None were seen in the upstream pool; one was taken in the downstream pool in a gill net (no other turtles of any kind were captured in the net). The remaining turtles at the type locality were taken in the riffle—some from the fastest water, most from water of medium depth and medium current, and none in a still backwater. About half of these were on clean sand or gravel bottom facing upstream. Others were on the downstream sides of rocks or actually under such rocks. In slower water, the turtles were in a greater variety of places (near dead wood, etc.).

About half of the *R. leukops* broke cover when we were 1 to 2 m away and swam off about as fast as we could pursue on a straight chase. However, typical escape behavior was a long rising curve and then an abrupt return to the bottom; if at this point a diver were directly over the turtle, it would reverse its course 180 degrees and swim away on the bottom. We consider *R. leukops* to be faster than any other Australian chelid, but *Elseya dentata* is almost as fast. The terminal reverse in escape behavior is virtually identical in all short-necked chelids (Legler has also observed it in kinosternids, emydids, and trionychids).

The short-necked species *Elseya dentata* and *Emydura krefftii* were also common in the river. Both occurred in the riffle, but *R. leukops* was the commonest turtle there. *Emydura krefftii* was most likely to be found in association with dead wood or undercut banks and was never in the fastest water. *Elseya dentata* tended to be in slower water but was seen or caught in the entire range of microhabitat described. *Chelodina longicollis* occurred in quiet, clear backwater situations where there were no *R. leukops* but where a few of the other short-necks were observed. We saw no *Elseya latisternum* in large rivers (Fitzroy and Dawson) at this latitude but found them to be common (with *Emydura krefftii*) in smaller tributary streams where there were no *R. leukops*.

Rheodytes leukops was also taken or seen on the Fitzroy River at Glenroy Crossing (23° 11'S, 149° 56'E), 3 to 4 km upstream from the type locality, and on the Dawson River, 2 km N Gainesford, Queensland (23° 47'S, 149° 46'E). Habitat at Glenroy Crossing was virtually identical to the riffle at the type locality. The Dawson River consisted of deep pools connected by shallower stretches in which there was no noticeable current; *R. leukops*, *Elseya dentata*, and *Emydura krefftii* were all found, in small numbers, in association with dead wood.

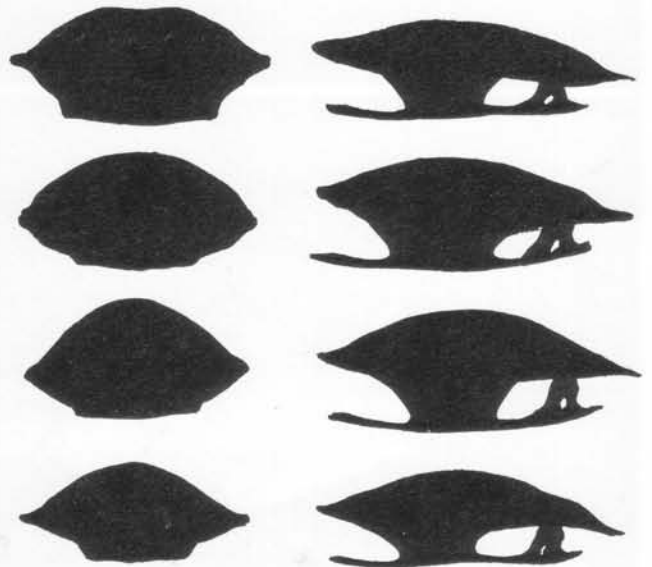


Figure 5. Optical cross sections and silhouettes of four short-necked chelids from eastern Australia (prepared from photographs); length and width of carapace (in millimeters) are given for each specimen. In order from top to bottom rows: *Elseya latisternum*, UU 17074♀, CL 271, CW 219; *Elseya dentata*, UU 17098♀, CL 309, CW 243; *Emydura krefftii*, UU 16909♀, CL 262, CW 200; *Rheodytes leukops*, paratype, UU 17118♀, CL 238, CW 196. All specimens obtained at or near the type locality of *R. leukops*.

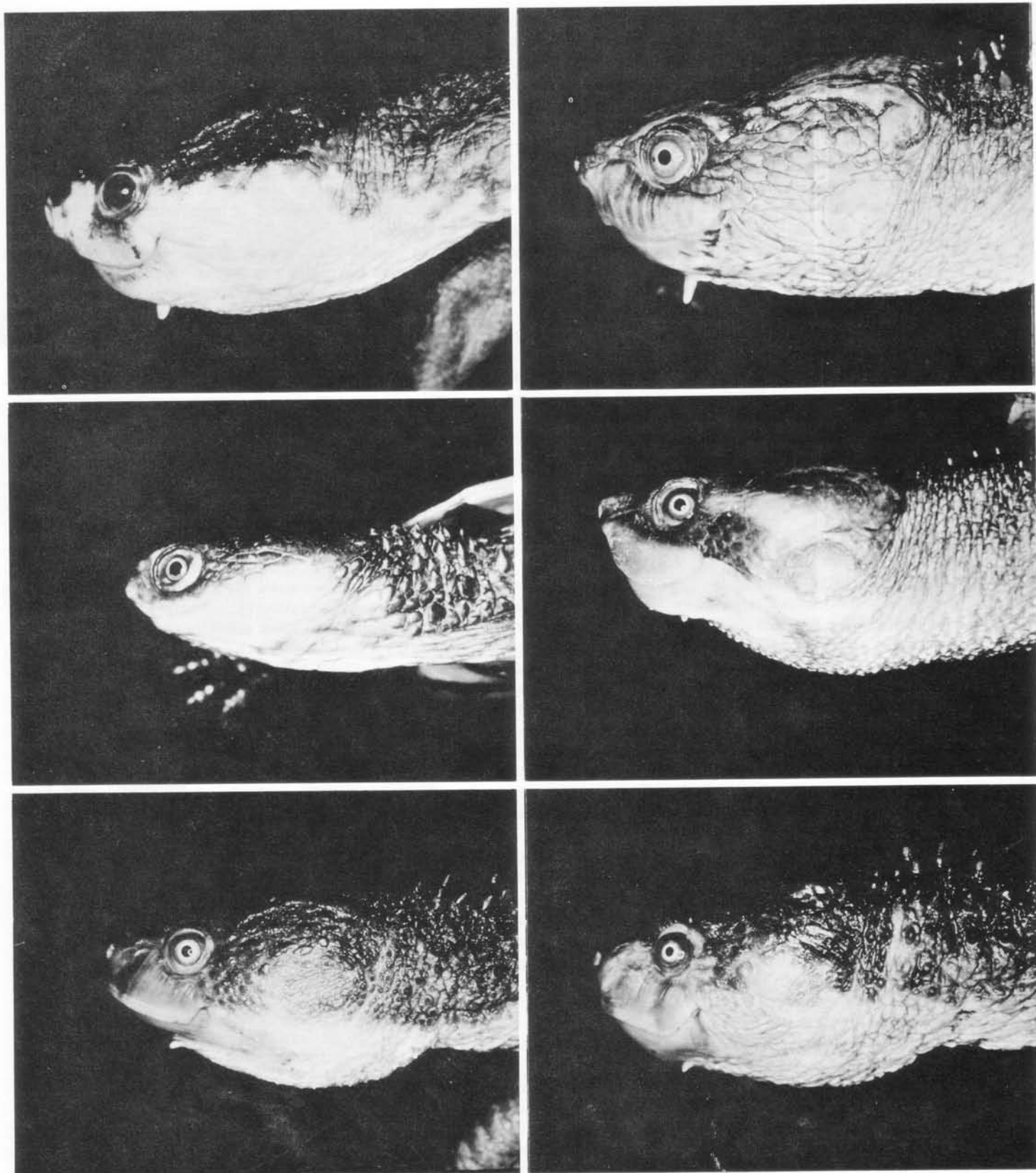


Figure 6. Heads of live short-necked Australian chelids, from left to right. Top row: *Elseya dentata*, UU 14862♀, Malanda, Queensland—note piebald coloration characteristic of old females; *Elseya latisternum*, UU 15131♀, Bloomsbury, Queensland. Middle row: *Pseudemydura umbrina*, A. Burbidge field number 46♂, Twin Swamps Reserve; *Emydura krefftii*♀ from the series UU 15881-8, Eton, Queensland. Bottom row: *Rheodytes leukops*, UU 17112♀, paratype; *Rheodytes leukops* UU 17107♂, paratype—note texture and coloration, which is typical of old males.

Table 5. Eggs of five species of chelids occurring on the Fitzroy River drainage system of Queensland. Mean and standard deviation are given above the extremes (in parentheses). Data for *Elseya dentata* are from other drainage systems. Annual reproductive potential is the sum of corpora lutea and potentially preovulatory ovarian follicles (minimum considers all follicles greater than 10 mm; maximum considers all follicles greater than 5 mm). Eggs from nest on Fitzroy R. are assumed, by elimination, to be those of *R. leukops*.

Species	Mean and Std. Deviation			Sample (N)		Incubation Time at 30.0°C	Annual Reproductive Potential	
	Weight (g)	Length (mm)	Width (mm)	Eggs	Clutches		Minimum	Maximum
<i>Rheodytes leukops</i>	7.50 ± 0.582 (4.70-9.84)	29.67 ± 0.969 (23.2-33.1)	21.17 ± 0.595 (19.0-23.8)	188	10	46.7 (44-50)	45.9 ± 6.25 (34-53)	58.6 ± 8.76 (44-70)
Nest on Fitzroy R.	—	30.7 (30.0-31.2)	21.8 (21.4-22.0)	5	1			
<i>Emydura krefftii</i>	9.75 ± 0.374 (8.74-11.35)	36.45 ± 0.936 (32.9-39.6)	21.13 ± 0.273 (20.0-22.4)	82	5	47.25 (46-48)	51.0 ± 15.79 (29-66)	56.2 ± 16.9 (35-75)
<i>Elseya latisternum</i>	12.05 ± 0.980 (11.22-15.70)	35.85 ± 1.320 (35.0-40.8)	23.98 ± 0.535 (23.2-25.7)	17	1	60.5 (60-61)	46	53
<i>Chelodina longicollis</i>	7.51 ± 0.384 (6.73-8.09)	30.81 ± 0.829 (29.0-32.0)	20.40 ± 0.272 (19.9-20.7)	12	1	67.0 (66-68)	24	33
<i>Elseya dentata</i>	15.7 —	48.6 (48.1-50.2)	27.7 (27.2-28.1)	5	1	160 (160-161)	Insufficient data	
				309	19			

DIET. Stomachs of eight fresh-caught live adults were flushed (Legler 1977) at the type locality on 7 October 1976. Stomach contents consisted purely of animal material and were entirely of insects except for fragments of freshwater sponge. Of these, the commonest were Trichoptera (larvae and pupae) of the families Helicopsychidae, Hydropsychidae, Hydropsilidae, and Leptoceridae, the first family being of commonest occurrence. By estimate, a single stomach might contain at least 100 larvae and their cases (most of which were uncrushed). Large aquatic lepidopteran pupae (Pyralidae?; 10 to 20 mm) were found in most of the stomachs and made up the bulk of the food in some stomachs. Lepidopteran larval cases were constructed partly of leaves, which were passed undigested in the feces. Dipteran and ephemeropteran larvae occurred as occasional items as did adult terrestrial coleopterans. Plant materials found in stomachs (bark, algal filaments, pieces of fibrous stem) were either closely associated with insect larvae or actually incorporated in their cases and were therefore assumed to have been ingested incidentally.

REPRODUCTION. A female obtained in mid-September was gravid, and 11 of the 18 females (61 percent) collected on 7-9 October were gravid. Eggs were obtained by hormonal induction of oviposition (Ewert and Legler 1978) or by dissection and were incubated under controlled laboratory conditions. All of the dissected females bore corpora lutea, indicating that they had produced at least two clutches of eggs by early October, and enlarged ovarian follicles, suggesting that they would produce at least one more clutch in the same season. Multiple clutches are, in fact, the rule for all species of chelids at this latitude (Legler, personal observation). The reproductive characteristics of five species of chelids occurring in the Fitzroy drainage are given in Table 5. Reproduction in Australian chelids will be the subject of a separate paper by Legler.

Two nests were found at the type locality; they had been constructed and robbed within the preceding 48-hour period (probably the previous night). Five eggs in one of the nests identified the nest (by elimination) as that of a *Rheodytes leukops*. One nest contained a slanting cavity with a maximum depth of 170

mm. The nests were on a flat sand and gravel bar approximately 9 m from the fast water of a riffle and slightly closer to some stagnant water. They were less than 1 m above the level of the flowing water.

BEHAVIOR OF YOUNG. Of the eggs incubated and hatched in Armidale, 26 juveniles (representing two clutches) were transported to the United States on 5 January 1977 and have been under observation in aquaria at the University of Utah since then. Several hatchlings from each of the same clutches were retained by Cann for observation in Sydney. An attempt was made to maintain captives in an environment like that (temperature and physical characteristics) of the original habitat.

Juveniles show a distinctive gregarious behavior, especially when no individual refugia are available (e.g., a bare aquarium or plastic bucket): They cling together, the claws of one grasping the shell of another—at various angles—to form a roughly spherical mass of individuals (Fig. 3). On some occasions, an entire clutch of hatchlings was involved in this clinging behavior.

Small juveniles spend much of their time under cover. They can conceal themselves effectively; in a 5-gallon (19-liter) tank containing 10 to 13 individuals, few can be seen. Rock caves and crevices are favorite retreats. When such retreats are not available, the turtles are quite capable of burrowing into the sand beneath a rock or piece of dead wood. Hatchlings were also observed burrowing into the sand without the aid of leverage from a rock; as they dig into the substrate, sand is thrown up and settles on the carapace. This behavior is reminiscent of sand burrowing in *Trionyx* and *Carettochelys* (personal observation) but not nearly as efficient.

The young are violently aggressive toward one another at times. This behavior could have been territorial, and it was nearly always observed on a feeding day (when most of the animals were out of their refugia). The behavior consisted of a visually oriented chase (begun in some instances from a distance of 15 cm) and violent biting of the head, neck, and forequarters of one juvenile by the other. The bitten animal did not

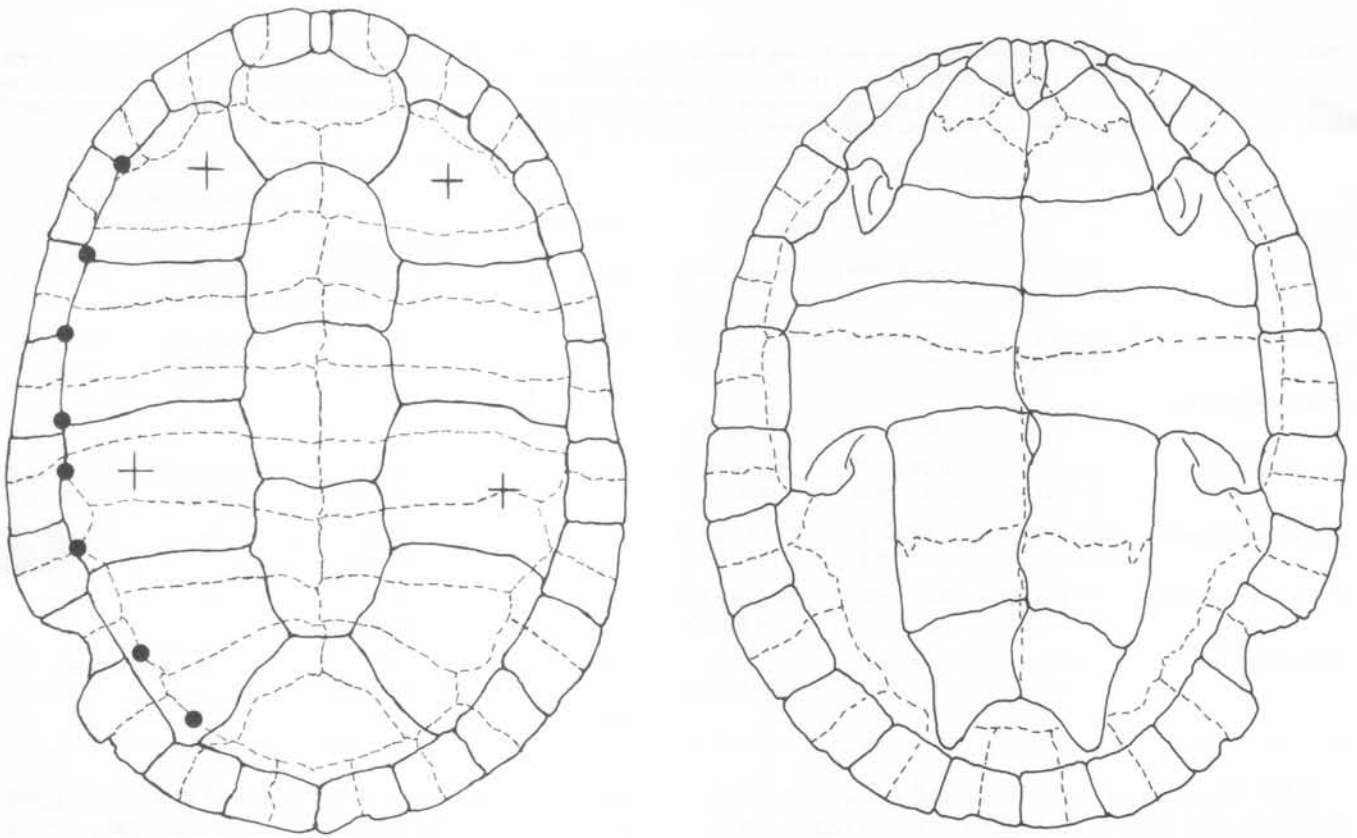


Figure 7. *Rheodytes leukops*, new genus and species: Paratype UU 17114♀, carapace length, 247 mm. Dorsal and ventral views of scuteless shell. Dots on left indicate where rib tips form gomphoses with peripherals. Small crosses indicate position of dorsal tips of plastral buttresses. The crescent-shaped break on left ninth marginal probably resulted from a *Crocodylus porosus* bite.



Figure 8. Type locality of *Rheodytes leukops* (Fitzroy River, 23°09'S, 149°55'E) looking downstream from the riffle. Water in left foreground is about 1 m deep and very fast; water near dead wood in right background is much deeper and slower. Two nests of *R. leukops* were found on the sandy area just to the right of this picture.

retaliate and was seldom chased very far. The dominant animal seemed not to return to any set place. Aggressive behavior was commonest just after feeding, occurred occasionally before feeding (and at other times) but never occurred during feeding (the animals were not fighting for food). Fighting after feeding lasted from 2 to 5 minutes, after which the turtles disappeared into refugia. Some refugia were shared by as many as three or four turtles.

When the small captives were active, they engaged in a lot of probing at the substrate with the snout. This probing seemed to involve both olfactory and visual cues. Although there was little or nothing for them to eat between feedings, they often stopped and bit at objects on rock faces (presumably algae). This behavior is tentatively interpreted as foraging. The hatchlings are easily able to move underwater objects at least ten times their own weight (average weight of hatchlings in April 1977, ca. 5.0 g); to do so, they first wedge the head and forelimbs under an object, then apply force with all four limbs. They moved the small half flower pots (50 g) that were supplied as caves about the aquarium in this way and were easily able to burrow completely into coarse gravel (individual stones 6 to 10 g).

The ability of young to secrete themselves in sand, gravel, and crevices probably explains our failure to find any immature stages at all in the field. This behavior also suggests some of the methods that the turtles use in foraging for insect larvae.

DISCUSSION

RELATIONSHIPS. The "short-necked" Australian chelids comprise the genera *Elseya*, *Emydura*, *Rheodytes*, and *Pseudemydura* (Figs. 6 and 9). Although the necks of these taxa are quite obviously relatively shorter than those of the "long-necks" (genus *Chelodina*), necks are quite difficult to measure accurately in live or preserved specimens. The groups are better categorized as follows:

Frontal bones fused; no parietosquamosal articulation; no posterior temporal arch; claws 4-4; intergular scute isolated from anterior free margin of plastron by anterior union of gular scutes; diploid chromosome number 54 (Bull and Legler 1980) *Chelodina*

Frontal bones separate; a parietosquamosal articulation forming a posterior temporal arch (or contributing to more extensive skull roofing in *Pseudemydura*); claws 5-4; intergular scute completely separating gular scutes (partly separating humerals) and contributing to anterior free edge of plastron; diploid chromosome number 50 *Short-necked taxa*

Of the short-necked taxa, *Pseudemydura* is rare (probably nearing extinction), isolated, and the least understood of the group (Burbidge 1967; Burbidge et al. 1974). Legler's studies of *Pseudemydura* (based upon all available specimens and to be reported elsewhere) suggest that it is not especially closely related to other short-necked Australian chelids. The genera currently recognized as *Emydura*, *Elseya*, and *Rheodytes* bear enough in common to be regarded tentatively as having common ancestry. In no case, however, is this similarity sufficient (in Legler's opinion) to warrant the lumping of these generic groups (Table 1).

Within the genus *Elseya*, there seem to be two major groups as follows: (1) *Elseya dentata* group—a series of populations (probably discontinuous) from the Burnett R. drainage, in the coastal lowlands and tablelands, northward and westward at least to the Victoria drainage of the Northern Territory; at least two Australian species; closely related to *Elseya novaeguineae* in New Guinea; (2) *Elseya latisternum* group—*Elseya latisternum* plus undescribed taxa in the Murray-Darling headwaters and eastern coastal drainages from approximately 32°S northward to the tip of Cape York and westward to approximately 140°E; possible relationships to undescribed taxa in New Guinea.

In the comparisons made in Table 1, the species names *Elseya dentata*, *Elseya latisternum*, and *Emydura krefftii* are used, but the characters discussed or compared are shared by the entire genus or proposed generic group.

MANDIBLE. Gaffney (1976) stated that the splenial bone was a common feature of chelids but occurred in no other extant group of chelonians. We have personally confirmed the occurrence of the splenial in all Australian chelids except *R. leukops*. Lack of a splenial would seem to be a derived character within the Family Chelidae. The shape of the prearticular in *Rheodytes* suggests that the splenial has become fused with that element (Fig. 2).

SEAM AND SUTURE CONTACTS. A midperipheral gomphosis for the rib tips of costals 2-4 occurs elsewhere in the Chelidae only in *Chelodina*; it is the usual condition in cryptodires. The same rib tips are interperipheral in all other chelids and in pelomedusids. Modal seam contacts on the posterior parts of M6 (75 percent of sample) and M8 (96 percent) are unique to *Rheodytes* among chelids; in other chelids, these contacts occur only as occasional variations, and they are rare among other living chelonians (Tinkle 1962; illustrations in Boulenger 1889).

We regard these two unusual situations in *Rheodytes* as related, derived characters. The relationships of lateral scutes to costal bones and of marginal scutes to peripheral bones remain fairly constant in all chelonians—the scutes tend to straddle the sutures in a way that seems to create maximal structural efficiency. However, either of these series may (and often does) shift upon the other. In *Rheodytes*, it is quite evident that the marginal-peripheral series has shifted anteriorly (or conversely the lateral-costal series has shifted posteriorly) for a distance equal to one-half the length of a peripheral bone in the bridge region. It is not clear what this shift has accomplished functionally or structurally.

CLOACAL BURSAE. One of our vivid early impressions of *Rheodytes* was that adults of both sexes swam with a widely gaping cloacal orifice (up to 30 mm in diameter). The orifice remains open when individuals are out of water. We first became aware of the large cloacal bursae when a female was examined in bright sunlight; the carapace transmitted enough light to illuminate the coelomic cavity and to produce a spectacular view internally for at least 100 mm, via the cloaca, revealing a large sac lined with a vascular, villous mucosa. We at first thought this was an oviduct, but dissection revealed it to be a large and unusual cloacal bursa. The structure and function of these organs is under investigation and is summarized elsewhere (Legler 1979). Water is pumped in and out of the bursae of captives and experimental animals at rates of 15 to 60 times per minute. Captives seldom breathe air, and we saw no heads

of *Rheodytes* at the surface under natural conditions. These facts suggest a respiratory function for the cloacal bursae. *Elseya dentata* also displays a gaping cloaca while swimming but has smaller cloacal bursae than *R. leukops*.

EYELIDS. The lack of a nictitating membrane is characteristic of all chelids (Legler, personal observation) and is unmentioned thus far in the literature. Early but brief mention of the translucent lower eyelid in *Chelodina* was made by Gadow (1909) and Walls (1942; "tertiary spectacle"). The anatomy of eyelids and the distribution of nictitating membranes in living chelonians is presently under study in Legler's laboratory.

ADAPTATIONS. *Rheodytes leukops* has relatively massive cervical vertebrae and a relatively small head in comparison to *Elseya dentata*. If the condylobasilar length of the skull is di-

vided by the sum of the lengths of the centra of cervical vertebrae 2-8, the following figures are obtained (mean, extremes, number of specimens): *Rheodytes leukops*—0.393 (0.38-0.40), $N = 3$; *Elseya dentata*—0.495 (0.47-0.52), $N = 2$.

The described structure of the skull and cervical vertebrae, the observations on behavior, and the examination of fresh stomach contents all strongly indicate that *Rheodytes* has become adapted to bottom probing and possibly the scraping of rocks and dead wood for insect larvae. The function of the pad of erectile tissue on the anterior part of the palate is unknown.

GEOGRAPHIC DISTRIBUTION. Localities for two of the paratypes in the Australian Museum collection are uncertain, and attempts to ascertain them more specifically have failed. Concerning AM R41794 ("Mackenzie River"), if this part of

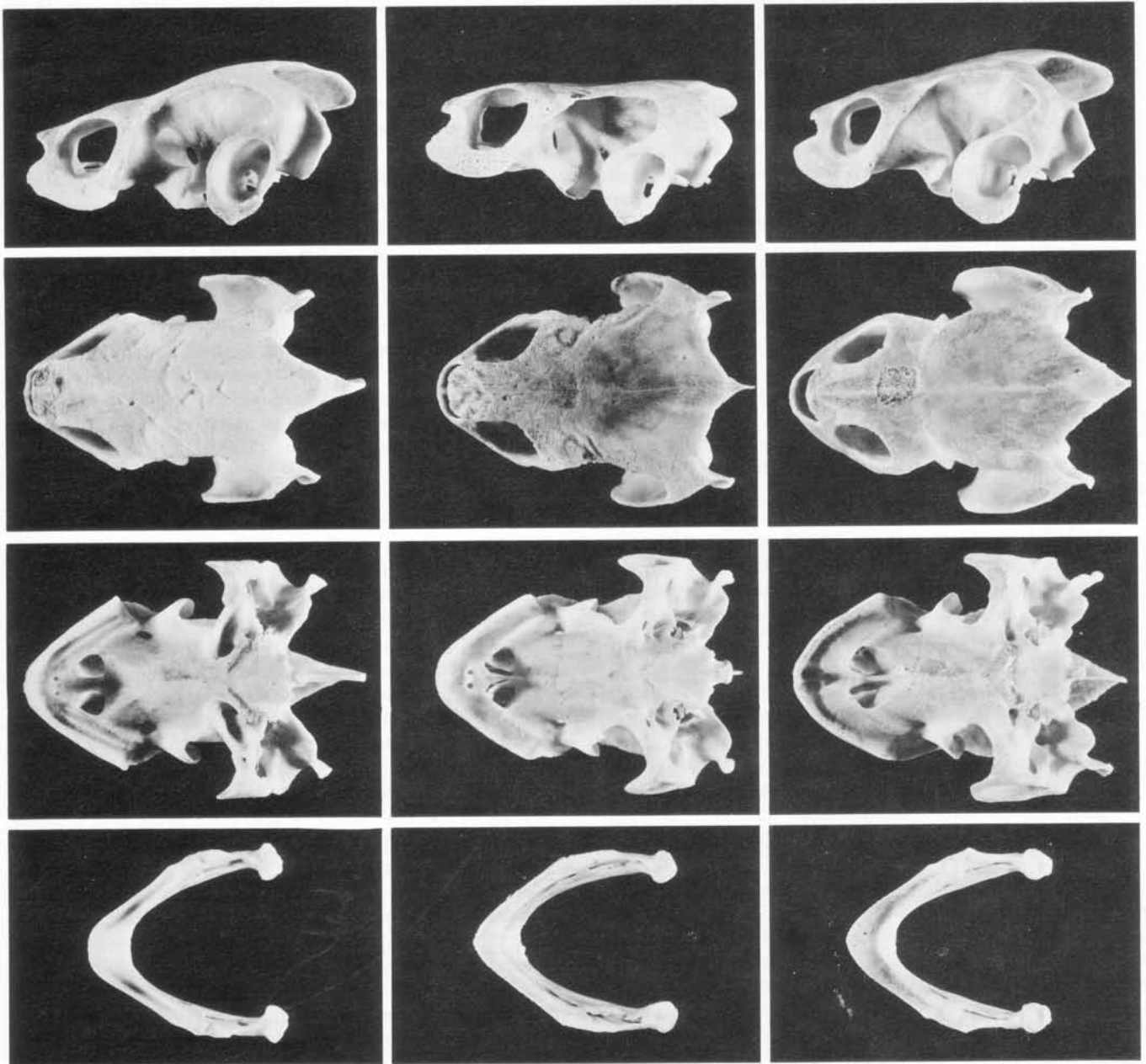


Figure 9. Skulls and mandibles of three species of short-necked Australian chelids, in vertical rows. Left: *Elseya dentata*, UU 14799♀, Auvergne, Northern Territory, condylobasilar length 64.5 mm. Middle: *Elseya latisternum*, UU 15037♀, northern New South Wales, CBL 46.3. Right: *Emydura krefftii*, UU 15650♀, Cooktown, Queensland, CBL 44.8.

the locality is correct, it establishes the presence of the genus in another major tributary of the Fitzroy River. The Mackenzie River begins at the confluence of the Nogoia and Comet Rivers, flows northeastward to its confluence with the Connors River and then southeastward to its confluence with the Fitzroy River (24° 24'S, 149° 53'E). AM R41274 was probably taken in the general region of the type locality (i.e., downstream from the confluence of all major tributaries). Except for the collection sites of these two specimens, all localities used in this description may be regarded as exact.

The specimens listed in this paper define the entire known range of *R. leukops* (Fig. 10). Little collecting has been done elsewhere on the Fitzroy drainage. *Emydura krefftii* was taken in traps (UU 15847-61) from the Nogoia River near Emerald, Queensland (23° 31'S, 148° 11'E), in July 1973, and a specimen of *Elseya dentata* (QM J28449) is known from the same locality. The river was murky and without current in 1973 when Legler observed it (due possibly to the first filling of Fairbairn Dam immediately upstream). It seems likely that, if *Elseya dentata* could survive in this kind of microhabitat, *Rheodytes*

could also. Some of the tributaries of the Connors River (ca. 22° 00'S, 148° 53'E) contain permanent, clear running water and may provide suitable habitat for *Rheodytes*. It seems virtually certain that *Rheodytes* occurs farther upstream in the Dawson River than here reported (say, southward at least to Taroom [25° 39'S, 150° 11'E], where *Elseya dentata* is known to occur [Legler, personal observation]).

It seems likely that *R. leukops* is confined to the Fitzroy drainage. We have observed, dived, and trapped in the Burnett drainage and short drainages between the Burnett and Fitzroy (e.g., Raglan Creek) to the south and in the Burdekin drainage and short drainages between the Burdekin and the Fitzroy to the north. Thus far, there is no evidence that *Rheodytes* occurs in any of these places.

COMPARATIVE MATERIALS EXAMINED

Legler's work on Australian chelids since 1972 has produced a collection of approximately 3,000 specimens (currently housed at the University of Utah but to be divided among that institu-

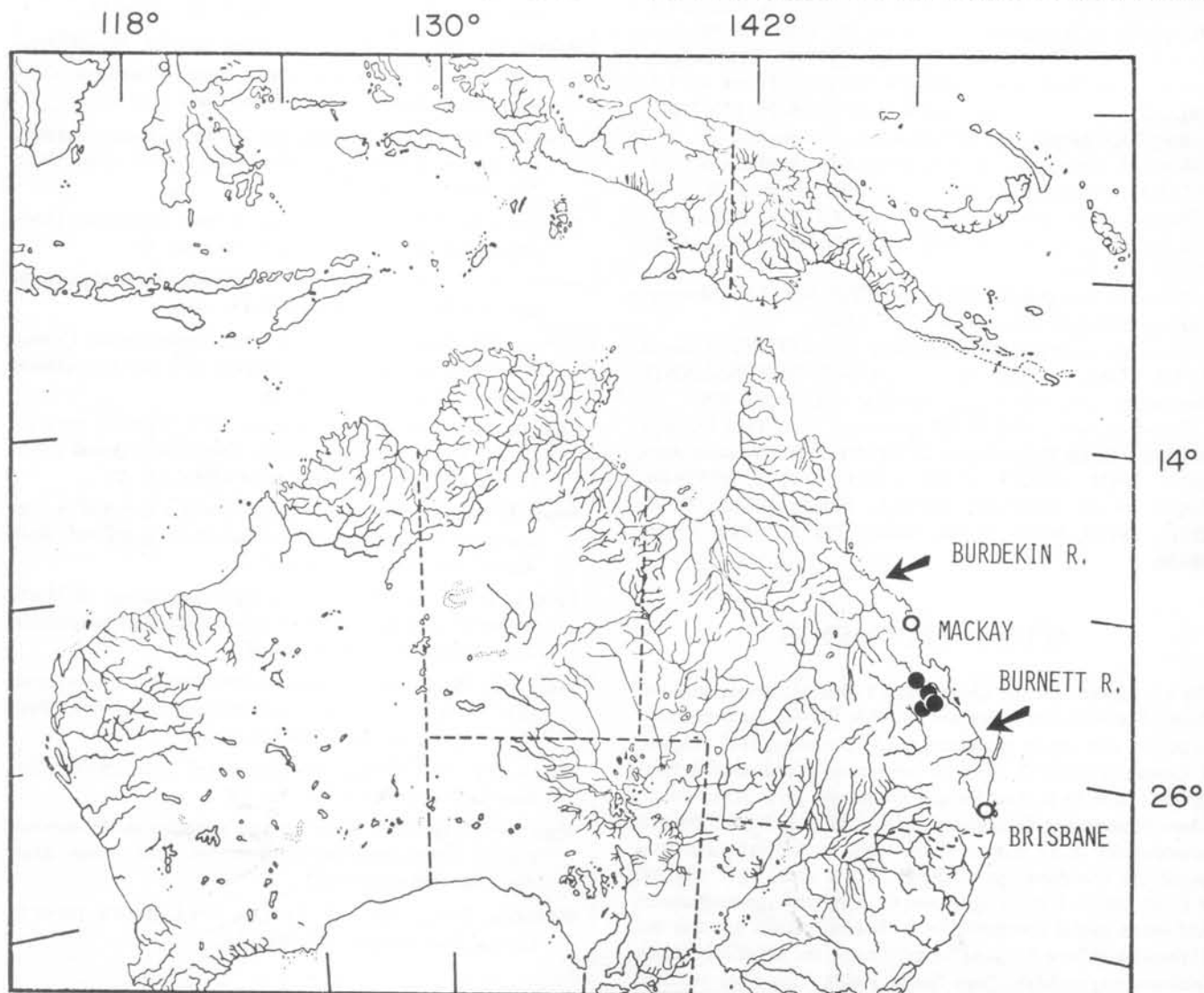


Figure 10. Known geographic distribution of *Rheodytes leukops*, new genus and species, in Australia. Localities from which specimens examined were taken are represented by four solid dots on the Fitzroy River and its tributaries. Arrows show mouths of Burdekin and Burnett Rivers. Circles showing MacKay and Brisbane are for orientation only. Drainage map of Australia adapted from Vari 1978.

tion and various Australian collections eventually). Data have been taken on approximately 1,500 other specimens in Australian and American museums. This large bank of specimens and data was consulted *ad libitum* in the preparation of this paper. Specimens used especially for the comparisons made in this paper are mentioned specifically in the text and legends and are listed below by major drainage system and museum number.

Elseya dentata. NORTHERN TERRITORY. Victoria R.: UU 14777, 14793-800; NMV 10386-90, 10397-99, 10403-6, 10828-30, 10832-35, 10847-48, 10850, 10859-60, 10870-74, 10885. Daly R.: UU 14809-844. Finnis R.: UU 14776. Adelaide R.: UU 14772-5. South Alligator R.: UU 14784-92. Roper R.: UU 14778-83. QUEENSLAND. Gregory R.: UU 14801-08. North Johnstone R.: UU 14845-71. Fitzroy R.: UU 17093-102. Burnett R.: UU 14872, 17085-92.

Elseya latisternum. QUEENSLAND. Cape York Peninsula: UU 14873-929. Mitchell R.: UU 14930-79. Endeavour R.: UU 14980-991. North Johnstone R.: UU 14994-15008. Burdekin R.: UU 15079. Andromache R.: UU 15124-51. Pioneer R.: UU 15081-123. Fitzroy R.: UU 17049-64, 17074-76. Raglan Cr.: UU 17070-73. Burnett R.: UU 15199-201, 17065-69. Brisbane R.: UU 15152-169. Nerang R.: UU 15170-71. Tallebudgera Cr.: UU 15172-98. NEW SOUTH WALES. Tweed R.: UU 15026-78, 17042-48. Richmond R.: UU 15009-25, 17077-80.

Emydura krefftii. QUEENSLAND. Normanby R.: UU 15674-722. Endeavour R.: UU 15619-673. Burdekin R.: UU 15723-32. Pioneer R.: UU 15867-98. Fitzroy R.: UU 15847-61, 16892-904, 16906-59, 16978-17029. Raglan Cr.: UU 16883-91. Burnett R.: UU 15834-46, 16866-882, 16905, 16960-77, 17066.

Emydura macquarii. NEW SOUTH WALES. Murray-Darling drainages: UU 15954-16085, 16863.

Emydura australis. NORTHERN TERRITORY. Victoria R.: UU 15462-95. Finnis R.: UU 15437-57. QUEENSLAND. Wenlock R.: UU 15319-69. Mitchell R.: UU 15371-405.

Pseudemydura umbrina. All specimens from Twin Swamps and Ellen Brook Reserves, ca. 29 km NE Perth, Western Australia: WAM 11092-3, 11386, 13385, 13744-5, 21559-64, 21859, 29320, 29337-40, 29342-3, 29345, 29348, 29350, 29376, 36159, 36179, 36338, 37495, 37977, 39040, 39956, 40535.

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LITERATURE CITED

- BOULENGER, G.A. 1889. *Catalogue of the chelonians, rhynchocephalians and crocodiles in the British Museum (Natural History)*. London.
- BULL, J.J., AND J.M. LEGLER. 1980. Karyotypes of side-necked turtles (Testudines: Pleurodira). *Canadian Jour. Zool.* 58:828-41.
- BURBIDGE, A.A. 1967. The biology of south-western Australian tortoises. Ph.D. Thesis, Univ. Western Australia, Nedlands.
- BURBIDGE, A.A., J.A.W. KIRSCH, AND A.R. MAIN. 1974. Relationships within the chelidae (Testudines: Pleurodira) of Australia and New Guinea. *Copeia* 1974(2):392-409.
- CANN, J. 1978. *Tortoises of Australia*. Sydney: Angus & Robertson (92 color photographs).
- CARR, A. 1952. *Handbook of turtles*. New York: Comstock Publ. Assn., Cornell Univ.
- EWERT, M.A., AND J.M. LEGLER. 1978. Hormonal induction of oviposition in turtles. *Herpetologica* 34(3):314-18.
- GADOW, H. 1909. *Amphibia and reptiles*. London: MacMillan.
- GAFFNEY, E.S. 1972. An illustrated glossary of turtle skull nomenclature. *Amer. Mus. Novitates* 2486.
- . 1976. Cranial morphology of the European Jurassic turtles *Portlandemys* and *Plesiochelys*. *Bull. Amer. Mus. Nat. Hist.* 157(6):487-544.
- LEGLER, J.M. 1976. Feeding habits of some Australian short-necked tortoises. *Victorian Nat.* 93(2):40-43.
- . 1977. Stomach flushing: A technique for chelonian dietary studies. *Herpetologica* 33:281-84.
- . 1979. Cloacal gills in Australian chelid turtles. 15 min. video tape and abstract. University of Utah Educational Media Service, Salt Lake City.
- LEGLER, J.M., AND R.M. WINOKUR. 1979. Unusual neck tubercles in an Australian turtle, *Elseya latisternum* (Testudines: Chelidae). *Herpetologica* 35(4): 325-29.
- SHAH, R.V. 1963. The neck musculature of a Cryptodire (*Deirochelys*) and a Pleurodire (*Chelodina*) compared. *Bull. Mus. Comp. Zool.* 129(6):343-68.
- TINKLE, D.W. 1962. Variation in shell morphology of North American turtles, 1: The carapacial seam arrangements. *Tulane Stud. Zool.* 9(5):331-49.
- VARI, R.P. 1978. The Terapon perches (Percoidei, Teraponidae): A cladistic analysis and taxonomic revision. *Bull. Amer. Mus. Nat. Hist.* 159(5):175-340.
- WALLS, G.L. 1942. The vertebrate eye and its adaptive radiation. *Bull. Cranbrook Inst. Sci.* 19.
- WILLIAMS, E.E. 1950. Variation and selection in the cervical central articulations of living turtles. *Bull. Amer. Mus. Nat. Hist.* 94(9):505-562.
- WINOKUR, R.M., AND J.M. LEGLER. 1974. Rostral pores in turtles. *Jour. Morph.* 143:107-119.

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