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A new species and subgenus of *Elseya* (Testudines: Pleurodira: Chelidae) from New Guinea

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Abstract

The New Guinea freshwater turtle, *Elseya novaeguineae* (senu lato) is a long-term, widespread resident of New Guinea and has been subject to substantial vicariance in one of the most geologically dynamic regions on earth. Thus, it should come as no surprise that the taxonomy of this turtle is poorly resolved. *Elseya novaeguineae* has long been recognized as a species complex, though which elements of this taxon warrant recognition as separate species has been debated. In this paper, we restrict *Elseya novaeguineae* to the Birds Head region of New Guinea, west of the Langguru Thrust and Fold Belt; we resurrect from synonymy *Elseya schultzei* for the populations north of the Central Ranges; and we describe a new species for the populations to the south of the Central Ranges. We revisit the classification of the genus *Elseya* throughout its range in the light of our work and recently published reports, and erect three subgenera that recognize the three major clades within this genus. Subgenus *Elseya* is the nominate subgenus, to which we assign *Elseya dentata*, *E. branderhorsti* and undescribed *E.* sp. aff. *dentata* [Sth Alligator]. *Elseya novaeguineae*, *E. schultzei* and our new species are assigned to a new subgenus, *Hanwarachelys*. Species of northern and eastern Queensland, *E. albagula, E. irwini, E. lavarackorum* and the fossil taxa *E. uberrima* and *E. nadibajagu,* are assigned to subgenus *Pelocomastes,* resurrected from synonymy.

Key words: *Elseya*; *Hanwarachelys*; *Pelocomastes;* Vogelkopf; Kikori; snapping turtles, New Guinea.

Introduction

The Chelidae is a family of side-necked turtles restricted to the continents of South America and Australia, including the islands of New Guinea, Timor and Roti. No representatives are known from outside their current range as fossils (Pritchard 1979), so the family is of clear Gondwanan origin. Chelid taxonomy until relatively recently was in drastic need of review (Cogger 2000). Surprisingly, given its remoteness, knowledge of species level taxonomy in New Guinea was long in advance of that of the larger and more accessible Australian continent to the south. The various taxa quickly came to the notice of science because they were food items regularly traded by the local peoples and so very familiar to them. Chelid turtles of the Australasian region reach their highest diversity in New Guinea, with three species of long-necked turtle (*Chelodina novaeguineae*, *C. reimanni* and *C. pritchardi*), two species of snake-necked turtle (*C. parkeri* and *C. oblonga* (formerly *rugosa*)), two species of snapping turtle (*E. novaeguineae,* and *Elseya branderhorsti*) and one species of short-necked river turtle (*Emydura subglobosa*) (Rhodin & Genorupa 2000; Georges & Thomson 2010). Six of these eight species are found in the Fly River drainage (Georges *et al.* 2006), all but one have clear and close affinities with sister species in Australia (Georges & Adams 1992;1996; Georges *et al.* 2002; Le *et al.* 2013; Todd *et al.* 2014), and all but one are restricted to the region of New Guinea south of the central ranges (Georges & Thomson 2010). The exception is *Elseya novaeguineae*, whose affinities within Australasia are less than clear and whose distribution extends throughout

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New Guinea, including the Birds Head, and associated islands of Waigeo, Misool and Aru (Georges *et al.* 2014) (Figure 1). Unlike other chelid species, *Elseya novaeguineae* is thought to be a long-term resident of the region that today forms New Guinea. The species has seen and been influenced by the orogenesis of modern New Guinea since the early accretion of island arcs to the north and well before the telescopic uplift of the central ranges (Georges *et al.* 2014), both of which resulted from the northern movement of the Australian tectonic plate and its subsequent oblique subduction beneath the Pacific plate.

Understandably, the taxonomy of *Elseya novaeguineae*, as a long term resident of New Guinea and subject to substantial vicariance in one of the most geologically dynamic regions on earth, is in need of further attention. *Elseya novaeguineae* was recognized as a species complex 100 years ago, with long standing confusion over the distinction between it and *E. branderhorsti* (Ouwens 1914), and the early discovery of distinctly different forms (Cogger 1972; Cann 1978; Rhodin & Genorupa 2000). Rhodin and Genorupa (2000) restricted the species to rivers draining to the north of the Central ranges, from the Popondetta region of northeastern Papua New Guinea in the east, to and including the Vogelkop Peninsula of northwestern Indonesian Papua (see also Iskandar 2000). Populations to the south of the central ranges were considered to be a separate species, based on unpublished work (Cann, 1978). These populations are restricted to the region from the Purari River region of PNG in the east to at least the Timika region of Indonesian West Papua in the west. Populations occupying the southern half of the Birds Head, in the rivers draining into Binaturi Bay, were considered to be a third species (Iskandar 2000; Rhodin & Genorupa 2000). Additional possible new taxa were thought to be each represented by populations in Tami River near Jayapura (*Elseya schultzei*), in northwestern Vogelkopf near Sorong, in the Sepik River, on the island of Waigeo, on the Islands of Aru (Rhodin & Genorupa 2000); and wetlands of the highland plains of Mt Jayawijaya (Iskandar 2000).

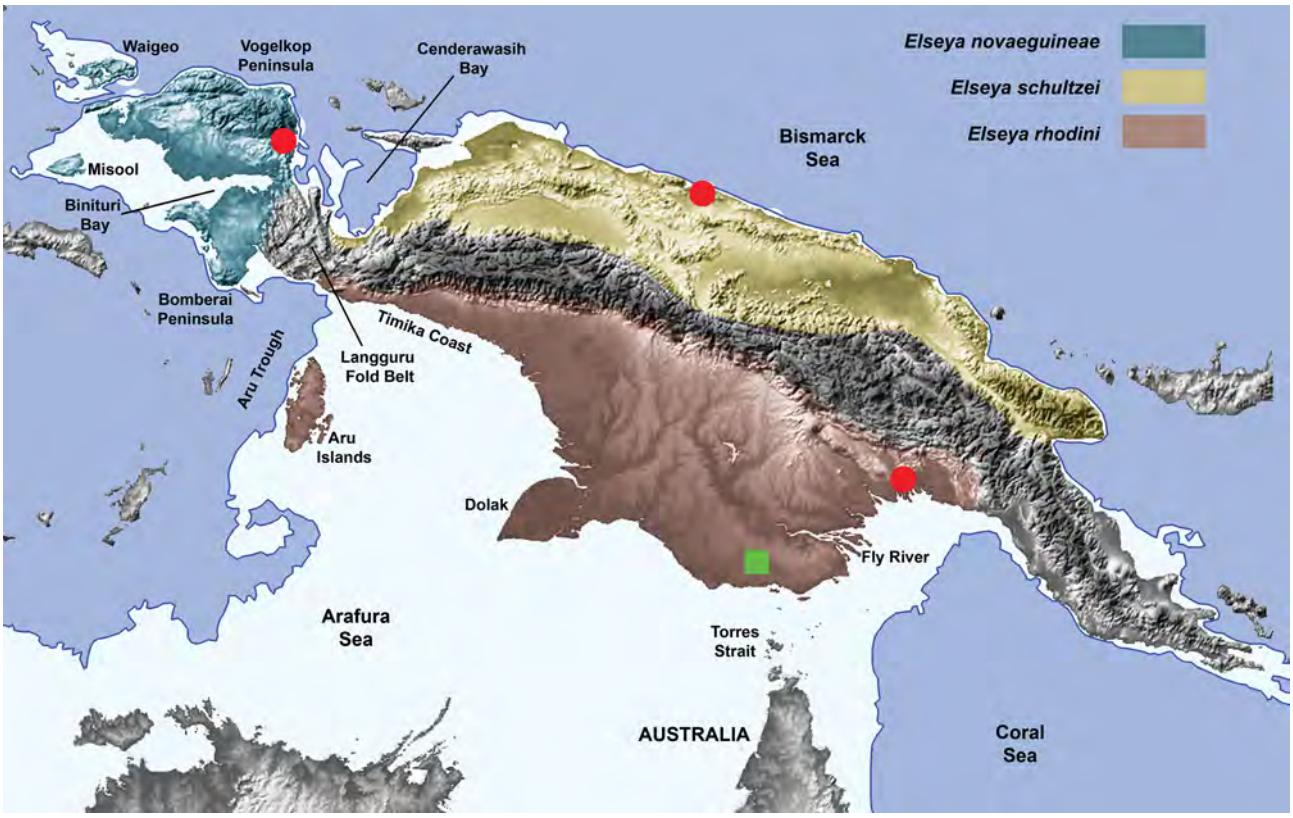

FIGURE 1. Map of New Guinea showing the distribution of *Elseya novaeguineae* (Birds Head), *E. schultzei* (north of Central Ranges) and *E. rhodini* (south of Central Ranges). The locations of the holotypes for each species are shown as red dots; the type locality for the neotype of *Elseya branderhorsti* is shown as a green square.

In this paper, we revisit these taxonomic issues, bringing together morphological and genetic data to: 1) delineate species within the *Elseya novaeguineae* complex and 2) describe a new species identified initially by Cann (1978: Plate 91) and Rhodin and Genorupa (2000) which we can restrict to the rivers south of the Central

Ranges of New Guinea. We resurrect the name *Elseya schultzei* (Vogt 1911: 410) from the synonymy of *Elseya novaeguineae* and restrict it to rivers north of the Central Ranges. We restrict the distribution of *Elseya novaeguineae* to the Birds Head region of Indonesian West Papua, which includes both the Vogelkopf and Bomberai peninsulas. The genus *Elseya* comprises three major clades, based on both morphological (Thomson *et al.* 1997) and molecular analyses (Georges & Adams 1992; Le *et al.* 2013; Georges *et al.* 2014). We also formalize recognition of these clades as subgenera and assign to them the extant species of Australia and New Guinea. We follow the nomenclature of Zangerl (1969) for the scutes and bones of the shell, with the modifications of Pritchard and Trebbau (1984) and Thomson et al. (1997).

List of Museum Acronyms: Museum für Tierkunde, Senckenberg Dresden—MTD; Museum für Naturkunde Berlin—ZMB; Natural History Museum London—BMNH, NHM; Papua New Guinea National Museum, Port Moresby—PNGM.

Genus *Elseya* Gray, 1867:44

Diagnosis: The members of the genus *Elseya* can be diagnosed by the following combination of external characters—head and neck, when extended, much shorter than the carapace; gular scutes entirely separated by the intergular scute; prominent alveolar ridge on the triturating surfaces of the jaw sheaths (secondarily reduced in *Elseya schultzei*, *E. novaeguineae* and *E. rhodini*); a horny casque (head shield) on top of the head of adults, entire, fragmented or deeply fenestrated; temporal region covered with prominent scales; front feet with five claws, rear with four claws. The anterior bridge strut of *Elseya* is angled sharply (approx. 45°) away from the rib/gomophosis of pleural one, a character shared with *Emydura* but excluding *Elusor*, *Pseudemydura*, *Rheodytes, Myuchelys* and *Flaviemys*. The anterior and posterior sides of the anterior bridge suture in *Elseya* are widely spaced both proximally and distally, with or without a medial constriction, whereas in *Emydura* only the proximal end of the suture is expanded followed by immediate constriction to a diameter confluent with the peripheral part of the bridge suture.

Systematics

Order: Testudines Batsch, 1788

Suborder: Pleurodira Cope, 1864

Family: Chelidae Gray, 1825

Subfamily: Chelodininae Baur, 1893

Genus: *Elseya* Gray, 1867:44

Subgenus *Elseya* Gray, 1867:44

The nominotypical subgenus, established by Thomson et al., this work. Type Species: *Elseya dentata* (Gray 1863: 98).

Diagnosis: A medial constriction in suture between the anterior bridge strut and the carapace; ileum sutures to the carapace on the posterior 2/3 of the 8th pleural (Figure 2); cervical scute absent except as a rare variant; parietal arch narrow; no prominent process of the head shield extending down the parietal ridge toward the tympanum; temporal region covered with prominent scales; temporal stripes absent; lingual ridge on the ramphotheca and the dentary bones absent; alveolar ridge moderately developed, narrow, clearly visible on the ramphotheca and the underlying dentary (Figure 3).

Referred species: *Elseya dentata* (Gray 1863: 98), *Elseya branderhorsti* (Ouwens 1914), *Elseya* sp. aff. *dentata* (Sth Alligator) (sensu Georges & Adams 1992). (Figure 4)

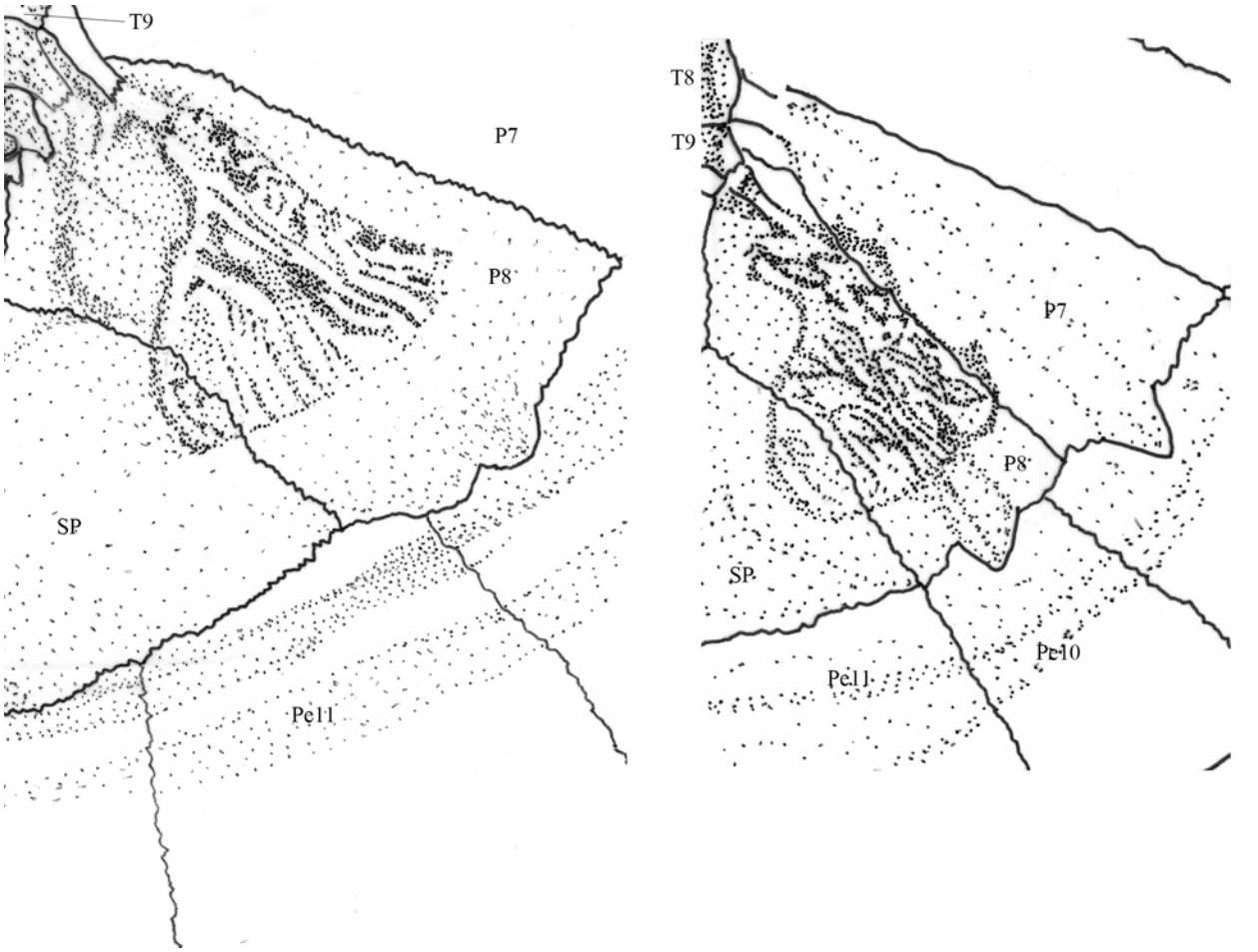

FIGURE 2. Comparison of the ileum suture of A. *Elseya branderhorsti* and B. *Elseya rhodini*. P7—Pleural 7, P8—Pleural 8, SP—Suprapygal, Pe10—10th Peripheral, Pe11—11th Peripheral, T8—8th Thoracic Vertebrae, T9—9th Thoracic Vertebrae.

Elseya dentata (Gray 1863: 98)

North Australian Snapping Turtle
1863 *Chelymys dentata*—Gray, 1863:98
1864 *Chelymys elseyi* —Gray, 1864, *nomen nudum* following Fritz and Havaš (2007).
1867 *Elseya dentata*—Gray, 1867. First use of combination.
1870 *Chelymys elseya*—Gray, 1870, *nomen nudum* following Wermuth and Mertens (1961).
1872 *Elseya intermedia*—Gray, 1872:23, holotype, BMNH 1947.3.4.14, from upper part of Victoria River, NT, Australia. Synonymy follows that of Cogger et al. (1983).

Type data: Lectotype—BMNH 1947.3.6.2 from Beagles Valley, Victoria River, Northern Territory (this study) (15˚ 34' S, 130˚ 54' E). Paralectotype—BMNH 1947.3.6.3 from Beagles Valley, Victoria River, Northern Territory (15˚34'S, 130˚54'E).

Diagnosis—Large short-necked chelid turtle. Juveniles have moderately spinose shells, reducing in prominence with age; many large adults with entire margin to the shell. Dark streaks or mottling of the otherwise cream plastron; carapace dark brown, almost black. Head shield entire, not as extensive or as fenestrated as the head shields of members of *subgenus Pelocomastes*. The alveolar ridge is moderate and does not increase the width of the triturating surface of the upper jaw in adults. Can be distinguished from all members of subgenus *Pelocomastes* by the medial constriction of the anterior bridge strut suture.

Distribution—Rivers below the Arnhem Land and Kimberley escarpments from the Daly River of the Northern Territory in the east to the Fitzroy River of Western Australia in the west. The eastern boundary of its distribution is uncertain, but it is not thought to be sympatric with *Elseya* sp. aff. *dentata* (Sth Alligator) of the Arnhem Land region.

FIGURE 3. Internal mouth parts of *Elseya branderhorsti* showing the alveolar ridge, present in *E.* (*Elseya*) secondarily lost in *E.* (*Hanwarachelys*).

Elseya branderhorsti (Ouwens 1914: 31) (Figure 4)

Branderhorst´s Snapping Turtle
1914 *Emydura branderhorsti*—(Ouwens 1914: 31)
1994 *Elseya branderhorsti*—(Bour, in David 1994: 81)

Type data—Holotype—lost. Original specimen from southeastern Papua, Indonesia, between the Lorentz River and Merauke, restricted this study. To avoid confusion, we hereby set PNGM R25201 (Figure 5), an adult female *Elseya branderhorsti,* as neotype for this species under article 75.3 of the ICZN Code. This specimen is lodged in the Papua New Guinea Museum in Port Moresby. The specimen is 424.7 mm in carapace length, collected from the Bensbach River of the Trans-Fly region of Papua New Guinea (8° 50' 58.6896" S., 141° 14' 52.944" E.) close to the locality of the original type that has been lost (explained below). The designated neotype is of the same species as that from the original description of Ouwens (1914). The species occurs in sympatry with the new species of *Elseya* described in this paper and it is therefore important to establish representative material for both species. We also refer a male specimen (PNGM R25202) as a second specimen collected at the same time and place as the neotype.

Diagnosis—Diagnosed by the following characters: prominent head shield, cervical scute absent, prominent alveolar ridge on the triturating surfaces, carapace usually uniformly dark, lacking any regular spots; plastron uniformly cream or yellow (white in hatchlings and small juveniles); iris typically indistinct, dark, similar in color to the surrounding sclera (liquid eyes); large adult size. Affinities lie with *Elseya dentata* in Australia.

Distribution—Lowland reaches of rivers in southern New Guinea, from the Lorenz River in the west to the Fly River in the east.

Collection History—This taxon was described as *Emydura branderhorsti* by Ouwens (1914) based on a single live adult specimen collected in "Southern New Guinea" by Dr. Branderhorst. The only comparative material was a single juvenile specimen of *El. novaeguineae* (Bogor Zoological Museum BZM 18) collected in "Northern New

Guinea" by Dr. Gjellerup (who worked in the Tami River area of Papua, Indonesia). The holotype was still alive in the Bogor Museum when described, but has since been lost (Leo Brongersma pers. comm. to John Goode 1967, 28 June 1963). The type locality of *El. branderhorsti* cannot be stated with accuracy, but it can be restricted through an examination of the travel history of Dr. Branderhorst, kindly brought to our attention by Anders Rhodin (unpubl. data).

Dr. Bastiaan Branderhorst's identity initially posed a mystery. There is no record of him at the Bogor Zoological Museum, nor could his name be found in any zoological literature referable to New Guinea. Through a painstaking search of early 20th century travel and botanical works on Dutch New Guinea, it was possible to establish his identity and reconstruct his New Guinea travels with some accuracy. Later, through the courtesy of Dr. S. Adisoemarto of the Bogor Museum, a reference was obtained which briefly summarizes some of this information (van Steenis-Kruseman 1950).

FIGURE 4. Live *Elseya* (*E*) *branderhorsti* (AA42043) male, from Marauke, PNG.

Bastiaan Branderhorst was born in Holland in 1880, received an M.D. degree in Utrecht in 1906 and spent 3 years from 1907 to 1910 as a military medical officer with the Dutch Army in Dutch New Guinea, serving under A.J. Gooszen and R.L.A. Hellwig, well-known explorers (Gooszen & Hellwig 1908; Hellwig 1908;1909; Anonymous 1910; Hellwig 1910b;a; Anonymous 1911; Heldring 1911). In addition to his medical duties his main pursuit was the collection of botanical and ethnographic specimens for the Buitenzorg (= Bogor) Museum (Heldring 1911; Valeton 1913). He collected several hundred plants and has at least 9 species of orchids and other exotic plants named after him (Smith 1910; Burck 1911; Harms 1911; Lauterbach 1911a;b; Pulle 1911; Smith

1911; Valeton 1911;1913; Smith 1914). Nowhere in the literature can any reference be found as to where he collected his turtle, but his plant localities are well documented, as are his travels. Specifically, he traveled extensively in southeastern Dutch New Guinea from the Lorentz River to the coast east of Merauke. Long excursions were made up the Lorentz, Eilanden, and Digoel rivers, where many plants were collected. Branderhorst left New Guinea in 1910, eventually settling into medical practice in Pengalengan, Java, where he apparently retired in approximately 1940.

From this information it is clear that the lost holotype of *Emydura branderhorsti* was collected somewhere in southeastern Dutch New Guinea, probably in either the Lorentz, Eilanden, or Digoel Rivers. The type locality is hereby restricted to "southeastern Papua, Indonesia, between the Lorentz River and Merauke".

Subgenus: *Hanwarachelys*, subgen. nov., Thomson et al., this study

Type species: *Elseya novaeguineae* (Meyer 1874:128)

Etymology: Formed from a combination of two Tok Pisin words (Pidgin, the lingua franca in New Guinea), *han* (= hand, arm, or branch) and *wara* (= water), that are used together (as *hanwara*) to denote a stream; and the Latin/Greek suffix commonly used for turtle genera *chelys* which means turtle. Hence it basically means "*stream turtle*" and is a reference to the generalized habitat preference of this group.

Diagnosis: The members of the subgenus *Elseya* (*Hanwarachelys*) can be diagnosed from other subgenera by the presence of a prominent head shield that extends down the parietal arch towards the tympanum, often contacting the tympanum. This has been seen as a feature separating *Myuchelys* from the *Elseya* (Thomson & Georges 2009), however in *Myuchelys*, the posterior process of the head shield also partially wraps around the top of the tympanum. Cervical scute present; alveolar ridge on the triturating surfaces absent or indistinct; lingual ridge absent; distinctive dark spots often present on major scutes of the carapace; iris distinct, differing in color from the surrounding sclera and the pupil; moderate adult size; ileum sutures to the carapace across the entire width of the 8th pleural, the anterior edge being adjacent to the suture between the 7th and 8th pleurals (Figure 2).

Referred species: *Elseya novaeguineae* (Meyer 1874), *Elseya schultzei* (Vogt 1911), *Elseya rhodini* (sp. nov. Thomson *et al*., this study).

External Morphology Osteology

Western New Guinea Stream Turtle

1874 *Platemys novaeguineae*—Meyer 1871:128
1888 *Emydura novaeguineae*—Boulenger 1888:450
1967 *Elseya novaeguineae*—Goode 1967:ix
1969 *Elseya latisternum novaeguineae*—Blackmore 1969:282
1974 *Elseya novaeguinea*—Burbidge et al. 1974:393 (ex-errore)
1985 *Elseya dentata novaeguineae*—Obst 1985:223
2015 *Elseya (Hanwarachelys) novaeguineae* (restricted, Thomson *et al*., this study)

Type data: Holotype—MTD D8222 from Passim, Barbussi River, ca. 3 km N. Sieb, 1 km S. Tandjung Sjeri (= Syeri), west shore Geelvink Bay (= Cenderawasih Bay), Papua, Indonesia (1˚41'S,134˚05'E), restricted this study.

Diagnosis—Eyes typically green in the sclera with little or no speckling, the iris is surrounded by a very bright gold ring. The head shield is entire, extending down the parietal arch and broadly contacting the tympanum. The gap in the head shield over the tympanic region is narrow with numerous small tubercles. The vomer does not contact the pterygoids or the premaxilla. Cervical scute is present and the lateral sulcus of the first vertebral scute contacts the middle of the second marginal.

Distribution—Streams draining into the rivers of the Vogelkopf and Bomberai peninsulas (the Birds Head) and associated offshore islands.

FIGURE 5. PNGM R25201 adult female *Elseya* (*Elseya*) *branderhorsti* photographed in life now at the Museum of Papua New Guinea, from the Bensbach River of Papua New Guinea (8° 50' 58.6896" S., 141° 14' 52.944" E.). Scale: 20 mm.

Collection History—The history of collection was kindly brought to our attention by Anders Rhodin (unpubl. data). This species was described by Meyer (1874) as *Platemys novaeguineae* based on a single specimen collected in “Neu-Guinea” without a specific locality, though the title of the work implied that it may have been collected in the Geelvink Bay area of New Guinea (northern present-day Papua, Indonesia). However, in a later work Meyer (1887) clarified the issue, stating that the specimen was collected at "Passim (Nordwest Neu Guinea)” which he also elaborated further as “Passim, Neu Guinea, am Westufer der Geelvinkbai” [Passim, west shore of Geelvink Bay, Northwest New Guinea]. This was noted by Boulenger (1888) who recorded the locality only as "Passim, Northwest New Guinea". Passim does not occur on any modern maps, and confusion has ensued regarding its exact location. Loveridge (1948) postulated that Passim was a misspelling of Pasi Island in Geelvink Bay. However, in another work, Meyer (1875) gave a detailed account of his trip to Geelvink Bay and provided a map which shows Passim located on the west coast of Geelvink Bay just northwest of Amberpon Island (= Rumberpon Island on current maps). He indicated that Passim was located at the mouth of the Barbussi River opposite Siari, just north of Rothes Cape. Though most of these localities are not to be found on modern maps, Siari (as "Sjari") is present on a more recent map of the area (Hellwig 1910b), and appears again as "Tandjung Sjeri" on an Australian map from 1971 and as Syeri on current maps from the late 1990s. Though Meyer's (1875) geographic coordinates for Passim were partly incorrect, the details of the shoreline on his map are quite accurate and identifiable, so that Passim can be identified on current maps as a small inlet just north of Sieb and south of Siari (= Tandjung Sjeri, = Syeri). The type locality of *Elseya novaeguineae* (Meyer 1874) should therefore be: Passim, Barbussi River, ca. 3 km N. Sieb, 1 km S. Tandjung Sjeri (= Syeri), west shore Geelvink Bay (= Cenderawasih Bay), Papua, Indonesia (1˚41'S,134˚05'E), and is hereby so restricted.

The type specimen of *El. novaeguineae* was considered as lost in Berlin by Goode (1967) who indicated as "? Syntype" a specimen in the Museo Civico di Storia Naturale in Genoa (MSNG CE8605, figured by Goode 1967: 62), this being a specimen collected by L.M. d'Albertis in Katow (= Mawatta, Western Province, Papua New Guinea), and originally noted by Boulenger (1888). However, Obst (1976) rediscovered, redescribed, and refigured Meyer's holotype of *El. novaeguineae* which is located in Dresden (MTD D8222) (Figure 4). Goode's "syntype" specimen therefore has no status as a type, and furthermore, the specimen represents a member of the new southern species being described in this paper. *Elseya novaeguineae* has been regarded as a distinct species with the exception of McDowell (1983) who placed it in synonymy his *Emydura dentata*.

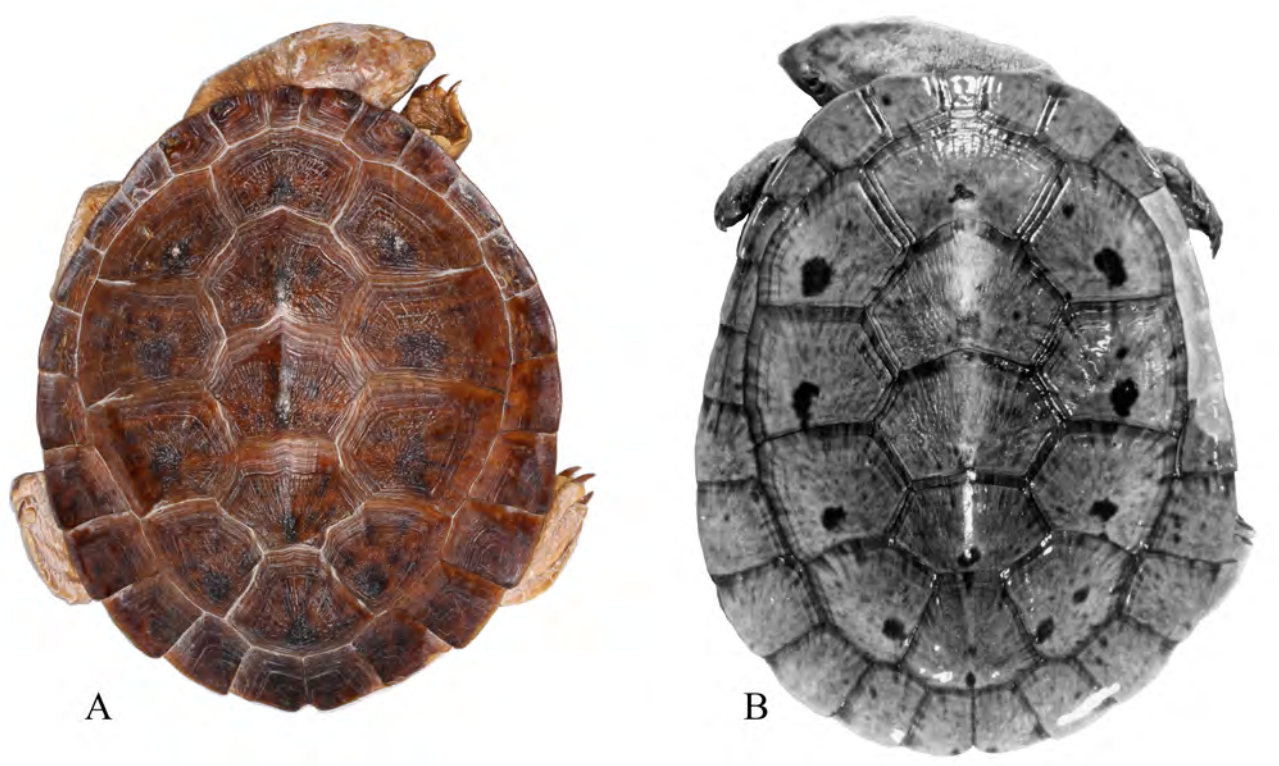

FIGURE 6. Dorsal views of the holotypes of A. *Elseya* (*H*) *schultzei* (ZMB 22182) and B. *Elseya* (*H*) *novaeguineae* (MTD D8222).

Elseya (*Hanwarachelys*) *schultzei* (Vogt 1911: 410) (Figure 6–7)

Northern New Guinea Stream Turtle

1911 *Emydura schultzei*—Vogt 1911:410
2000 *Elseya schultzei*—Samedi and Iskandar 2000:111
2010 *Myuchelys novaeguineae*—Georges and Thomson 2010:29
2010 *Elseya novaeguineae*—Rhodin et al. 2010:131
2015 *Elseya* (*Hanwarachelys*) *schultzei* resurrected, Thomson et al. this study

Type data: Holotype—ZMB 22182 collected near Sae village, Seko coast, near Skosai, ca 5 km W. mouth of Tami River, Papua, Indonesia (2˚37'S,140˚54'E), restricted this study.

Diagnosis—Eyes typically green in the sclera with a bright gold iris which is distinct. Head shield entire, extending down the parietal arches to broadly contact the tympanum. Head shield narrower than in *Elseya novaeguineae* but wider than in *E. rhodini*. No contact between the vomer and the pterygoids of the skull, distinguishing the species from *E. rhodini.*

Distribution—Streams draining into the rivers of New Guinea north of the central ranges—i.e. not including the Vogelkopf and Bomberai peninsulas (Birds Head)—and east to at least Madang.

Collection History—This taxon was described by Vogt (1911) based on a single specimen collected by Leonhard Schultze in an unnamed river west of the Tami River in northeastern Papua, Indonesia (type locality "Fluss westlich der Tamimündung" [river west of the mouth of the Tami]). Although it is impossible to give a precise locality, Schultze (1914) gave an account of his travels and a detailed map from which one can deduce that the type specimen was probably collected near Sae village, Seko coast, near Skosai, ca 5 km W. mouth of Tami River, Papua, Indonesia (2˚37'S,140˚54'E); and the type locality is hereby so restricted. The holotype is in the Berlin collection (ZMB 22182, figured by Goode 1967). When described, *Emydura schultzei* was compared to and distinguished from a specimen of "*Emydura macquariae*" (ZMB 22210, figured by Goode 1967:67) from the upper Sepik River basin south of the headwaters of the Tami River, near the Indonesia-Papua New Guinea border. The species was recognized as distinct until synonymized with *E. novaeguineae* by Goode (1967). That *E. schultzei* represents a distinct taxa has been confirmed by recent genetic studies (Georges *et al.* 2014). Therefore we remove this species from the synonymy of *Elseya novaeguineae* recognizing it as a valid taxon.

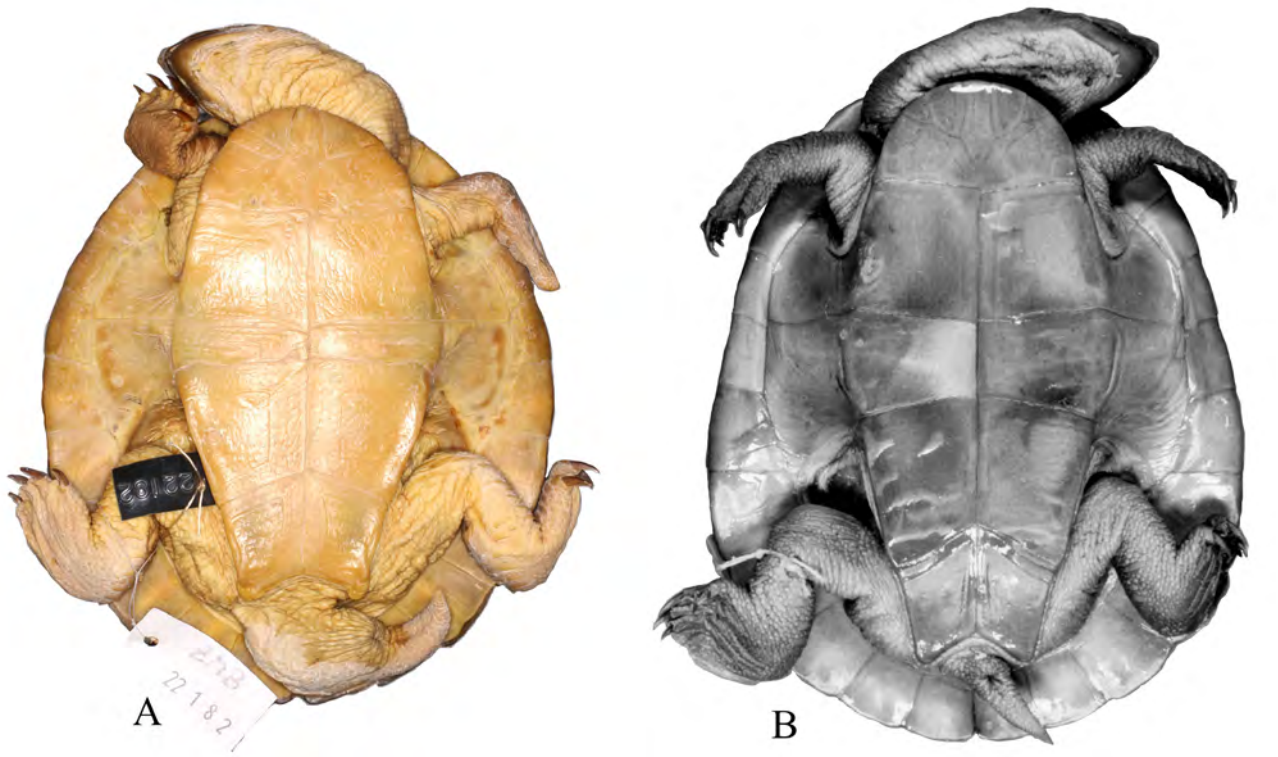

FIGURE 7. Ventral views of the holotypes of A. *Elseya* (*H*) *schultzei* (ZMB 22182) and B. *Elseya* (*H*) *novaeguineae* (MTD D8222).

***Elseya* (*Hanwarachelys*) *rhodini* sp. nov.**

Southern New Guinea Stream Turtle
2015 *Elseya rhodini* sp. nov., Thomson et al., this study.

Type data: Holotype—PNGM R25204 (Figure 8), adult female (carapace length: 255 mm), collected at Rue Creek (tributary of Wau Creek), Gulf Province, Papua New Guinea (07˚11' 67.3" S, 144˚37' 13.8" E) by Yolanie Amepou on 6 January, 2015 (Figure 9). Paratype: PNGM R25203, adult male (carapace length: 205 mm), herein set as Allotype, collection data as per Holotype. For basic measurements of these types and others from the genus *Elseya* see Table 1.

Etymology—Named in honor of Anders G. J. Rhodin; Chairman Emeritus of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group; Founder and Director, Chelonian Research Foundation. He also researched the turtles of Papua New Guinea describing two species, *Chelodina* (*M.*) *parkeri* (Rhodin and Mittermeier, 1976) and *Chelodina* (*C.*) *pritchardi* (Rhodin, 1994). He was also one of the first to collect this new species (Rhodin and Rhodin, 1977), and the first to recognize it as new (Rhodin and Genorupa 2000).

Distribution—Streams draining into rivers in New Guinea, south of the central ranges, from the Sitekwa River region of Papua, Indonesia, to the Kikori-Purari rivers region of Papua New Guinea. Aru Islands. (Figure 1)

Diagnosis –Distinguished by gold speckling usually present in the sclera of the eye, which partially obscures the iris; base color green (Figure 10). In *Elseya novaeguineae and Elseya schultzei* the sclera is bright green and the iris is starkly contrasted, though the base colors of the sclera in the later is a duller and plainer green. The head shield in *E. rhodini* is reduced when compared to other species of this subgenus. The lateral edge of the head shield at its midpoint between the eye and the tympanum is above the level of the eye, below it in the other species. The ventral extension of the head shield down the parietal arch is also reduced, typically still reaching the tympanum, but narrower throughout its length. Posterior to the eye in *E. novaeguineae* and *E. schultzei* is a variable but generally present extension of the head shield that extends down behind the eye, in some specimens to nearly the midpoint of the eye. This is absent in *E. rhodini*. On the carapace the spots on the scutes of *E. rhodini* are visible in all growth stages, whereas in the other two species they are often faded or absent in adults. The cervical is generally present in the members of this group however it is narrower (approximately 30% of length) in *E. rhodini* whereas it is usually 50% of length in the other two species. The lateral sulcus of the first vertebral scute in both *E. schultzei* and *E. novaeguineae* contacts the center of the second marginal scute, whereas in *E. rhodini* it contacts the anterior ¼ of the second marginal. The skull of *E. rhodini* can be diagnosed by the contact of the vomer with the pterygoids posteriorly and the premaxillae anteriorly.

Description

External Morphology

Carapace—The carapace is broadly oval slightly flattened at the anterior from the 2nd marginal. The first vertebral scute is approximately the same width as the second. The outer sulci of the first vertebral tend to intersect the 2nd marginal close to the sulcus between the 1st and 2nd marginal, differing from *E. novaeguineae* where it is in the center of the 2nd marginal. There is some flaring of the marginal over the hind legs, though it tends to be more pronounced in *E. novaeguineae* and *E. schultzei* than is apparent in similarly sized individuals of *E. rhodini*. Cervical scute is present for all three taxa, though it is usually relatively narrower in *E. rhodini* than in the other two species of the subgenus. The carapace is brown in color for all three species, spots may be present at the center of each major scute, these persist into adult hood in *E. rhodini*, are faded if present in *E. schultzei* and may be absent altogether in *E. novaeguineae*.

Plastron—The plastra of all three species are very similar, being rectangular in general shape but widest at the posterior of the anterior lobe and with lateral flanging in older individuals just anterior to the rear legs on the posterior lobe. The plastral formula is generally pec>fem>abd>ana>int>hum with the gulars excluded from the midline by the intergular. The plastron is cream to yellow in color, very occasionally there is a slight pink suffusion.

Head and soft parts—The color of the sclera of *E. rhodini* is gold flecked green, 2.5Y7/8 to 2.5Y8/8 (Munsell 2000) with the iris gold and relatively indistinct. Compared with the color of the sclera of *E. novaeguineae* is green with no flecks, 5y7/3 to 5y8/3 (Munsell 2000) with a very distinct gold iris, and in *E. schultzei* it is also green with no flecks, 5y7/6 to 5y8/6 (Munsell 2000) again with a very distinct gold iris. The dorsal surface of the head of *E. rhodini* is variegated in color between yellow brown to dark brown, a similar pattern is seen in *E. schultzei*, however *E. novaeguineae* tends to be far less variegated without the striking patterns seen in the other species.

FIGURE 8. Dorsal, ventral and lateral views of the holotype PNGM R25204 of *Elseya (Hanwarachelys) rhodini* from Wau Creek, Kikori Drainage, Papua New Guinea. Scale: 20 mm.

Size and Sexual Dimorphism—This species attains a size of approximately 240mm carapace length with females being slightly larger than males. This is similar for all members of the subgenus *Hanwarachelys*. The species attains a smaller adult size than *Elseya branderhorsti* with which it is sympatric throughout parts of its range.

FIGURE 9. Habitat of *Elseya rhodini* Wau Creek, Sirebi River, Kikori drainage (07˚11' 67.3" S, 144˚37' 13.8" E).

FIGURE 10. Lateral view of the head of *Elseya rhodini*. Wild caught individual (UC<Aus>AA42045).

Osteology

Skull (Figs. 11–13)—Dermal roofing elements of the skull are similar in all species of *Elseya*, the frontals are paired and the anterior process separates the nasals almost in their entirety. Parietals are large and postero-laterally suture to the squamosal to form the parietal arch. The arch is narrow in the *Elseya* (*Elseya*) much wider in *Elseya* (*Hanwarachelys*). This feature also determines the degree of lateral extension of the head shield as it requires bone for its support.

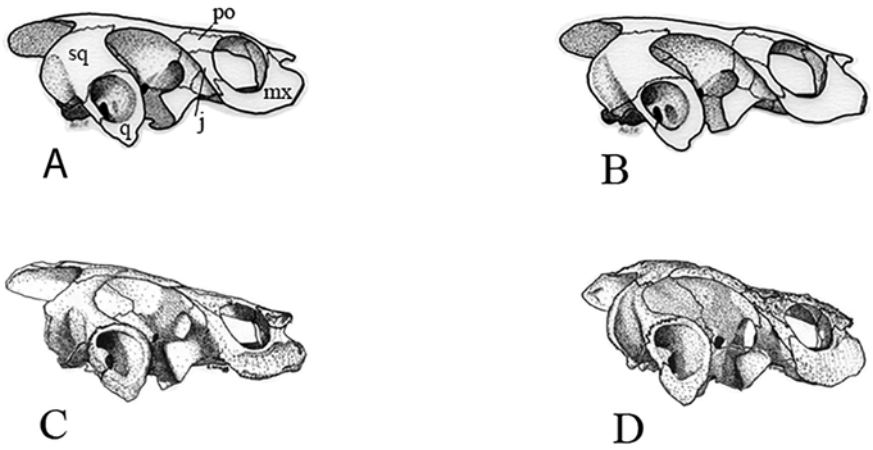

FIGURE 11. Lateral views of the skulls of A. *Elseya* (*Hanwarachelys*) *rhodini*, B. *Elseya* (*Hanwarachelys*) *novaeguineae*, C. *Elseya* (*Elseya*) *dentata*, and D. *Elseya* (*Pelocomastes*) *albagula*. po—postorbital, sq—squamosal, q—quadrate, j—jugal, mx—maxilla.

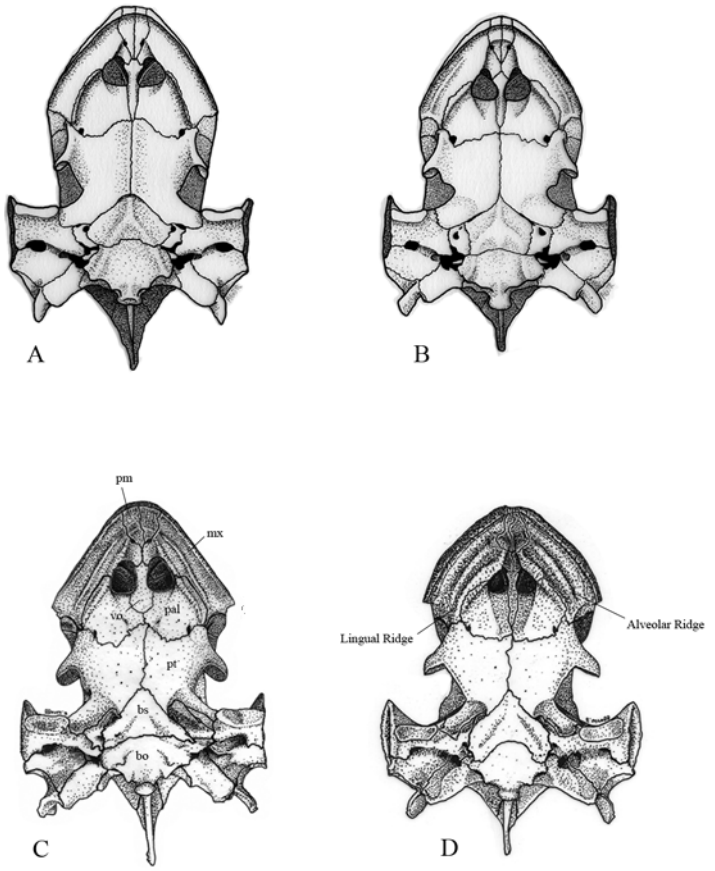

FIGURE 12. Ventral views of the skulls of A. *Elseya* (*Hanwarachelys*) *rhodini*, B. *Elseya* (*Hanwarachelys*) *novaeguineae*, C. *Elseya* (*Elseya*) *dentata*, and D. *Elseya* (*Pelocomastes*) *albagula*. pm—premaxilla, mx—maxilla, pal—palatine, vo—vomer, bs—basisphenoid, bo—basooccipital. Also labelled are the alveolar and lingual ridges.

On the palatal surface there are significant differences at the species level. The vomer of *E. rhodini* completely divides the maxillae anteriorly to meet the pre-maxillae and posteriorly the palatines to meet the pterygoids. In *E. novaeguineae* both the maxillae and palatines meet at the midline. In the description of *Elseya* (*Pelocomastes*) *albagula* (Thomson et al, 2006) the form of the alveolar ridge was further defined and we follow this here. The lingual ridge (sensu Thomson et al, 2006) is completely absent in all members of both *Elseya* (*Elseya*) and *Elseya* (*Hanwarachelys*) its presence being a synapomorphy for the *Elseya* (*Pelocomastes*). However the alveolar ridge is present in members of the *Elseya* (*Elseya*) and is only partially present in the members of *Elseya* (*Hanwarachelys*). In *E. rhodini* there is no obvious alveolar ridge on the ramphotheca of the upper jaw whereas there is a reduced, though present ridge consisting of a row of raised nodules in *E. novaeguineae*.

Cervicals—The articulation formula is the same in all three species and follows the typical chelid condition of (2(3(4(5)6)7(8) (sensu Williams 1950).

Shell—The carapace of members of the *Elseya* (*Elseya*) differ from members of the *Elseya* (*Hanwarachelys*) in the structure of the bridge strut suture , the former having a medial constriction, present in all three species, whereas this is absent in all members of the latter. Further the sutural scar of the ileum in the *E.* (*Elseya*) is separated from the anterior suture of the 8th pleural with this scar occupying the posterior 2/3 of the 8th pleural and continuing onto the pygal. In *E.* (*Hanwarachelys*) this scar is adjacent to the anterior suture of the 8th pleural occupying the full width and also continuing on to the pygal (Figure 2). All members of the *E.* (*Hanwarachelys*) normally possess a cervical scute, absent in *E.* (*Elseya*) and *E.* (*Pelocomastes*).

All three species of *Elseya* (*Hawarachelys*) lack exposed neural bones (sensu Thomson & Georges 1996) a feature common to the entire genus. There are slight differences in the general morphology of the shell between the three species within *E.* (*Hanwarachelys*), but subject to considerable within species variation.

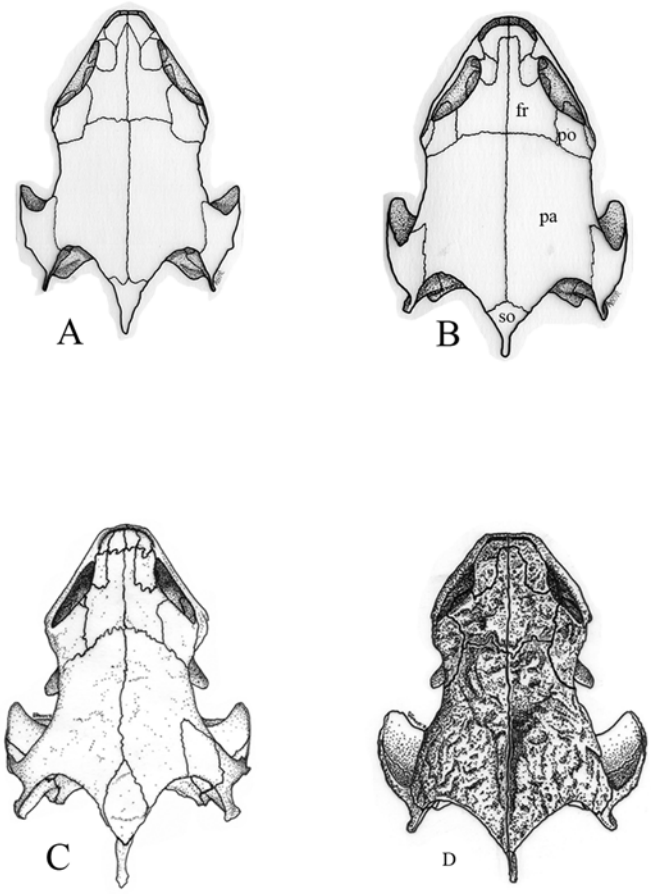

FIGURE 13. Dorsal view of the skulls of A. *Elseya* (*Hanwarachelys*) *rhodini*, B. *Elseya* (*Hanwarachelys*) *novaeguineae*, C. *Elseya* (*Elseya*) *dentata*, and D. *Elseya* (*Pelocomastes*) *albagula*. fr—frontal, po—postorbital, pa—parietal, so—supraoccipital.

Subgenus: *Pelocomastes* (de Vis 1897) resurrected, this study.

Type Species: *Elseya uberrima* (de Vis 1897) sensu Thomson (2000).

Diagnosis: This subgenus can be diagnosed by the presence of extensive lingual ridges in addition to the alveolar ridges present on both the ramphotheca and the underlying dentary. The complete absence of a medial constriction in the anterior bridge strut and in part by the presence of the ileum suture being in contact with the suture between the 7th and 8th pleurals. The head shield is deeply fenestrated but does not extend down the parietal arch towards the tympanum. Cervical scute is typically absent and the first vertebral scute is wider than the second.

Referred Species: *Elseya uberrima* (de Vis 1897), *Elseya lavarackorum* (White & Archer 1994), *Elseya irwini* (Cann 1997), *Elseya albagula* (Thomson *et al.* 2006), *Elseya nadibajagu* (Thomson & Mackness 1999), *Elseya* sp. aff. (Daintree) (sensu Todd *et al.* 2014). (Figure 1)

Multivariate Analysis

Stepwise canonical discriminant analysis (SAS_Institute 1988) was used to determine the distinctiveness of *Elseya* (*Hanwarachelys*) *rhodini* and its two closest relatives, *E. novaeguineae* and *E. schultzei*. Head measurements were expressed as a ratio of head length (HL); head length and all shell measurements were expressed as a ratio of carapace length (CL). Measurements and the abbreviations used here were defined by Thomson *et al.* (2000) and applied to the description of *Elseya* (*Pelocomastes*) *albagula* (Thomson *et al.* 2006).

Elseya species are generally conservative in their morphology within the subgenera, hence we present here the analysis of the subgenus *Hanwarachelys*. Within this group the differences between the species was far greater than that seen in sexual dimorphism, hence we present an analysis that combines both males and females.

Discrimination between the three taxa was good, with no overlap in the plot of can1*can2 (Figure 14). Two ratio variables provided the highest discrimination; VT/HL (partial $R^2 = 0.20$, $F = 3.44$, $p < 0.05$); OD/HL (partial $R^2 = 0.17$, $F = 2.85$, $p < 0.08$) demonstrating that skull shape contributed significantly to discrimination between the three taxa. Canonical Variante 1 explained 89.18% and Canonical Variante 2 explained 10.82% of the variation among group centroids. In terms of Generalized Mahanobalis Distance, *E. rhodini* was 58.3 units from *E. novaeguineae* and 13.5 units from *E. schultzei*. In resubstitution analysis, 100% of the *E. novaeguineae* and *E. rhodini* were correctly assigned to species with 1 specimen of *E. schultzei* misidentified as an *E. rhodini*. Under crossvalidation 83.3% of *E. novaeguineae*, 67.7% of *E. rhodini* and 70.0% of *E. schultzei* were correctly classified; with the priors at 0.33 all species were correctly assigned.

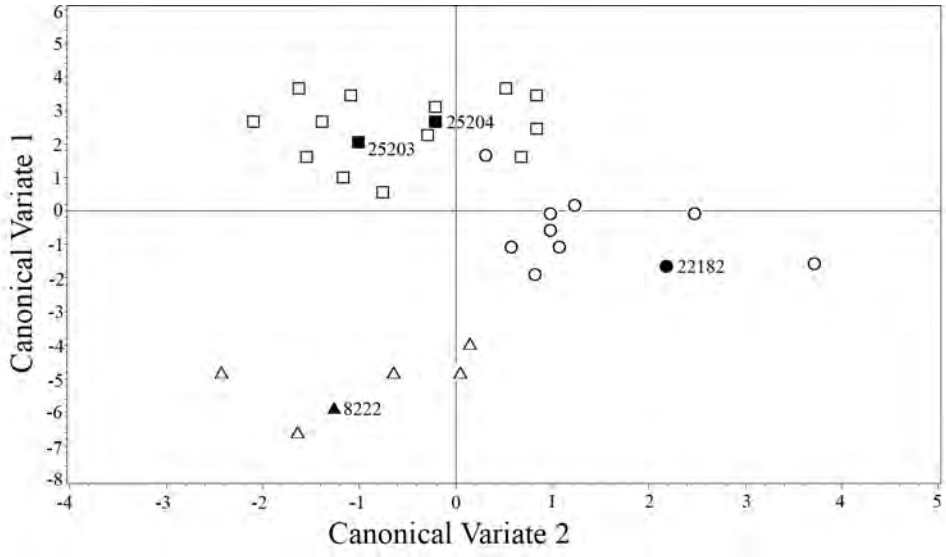

FIGURE 14. Discriminant Function Analysis (DFA) using SAS. Showing Canonical Variante 1 vs Canonical Variant 2 for the three Papuan species in the *Elseya novaeguineae* complex.

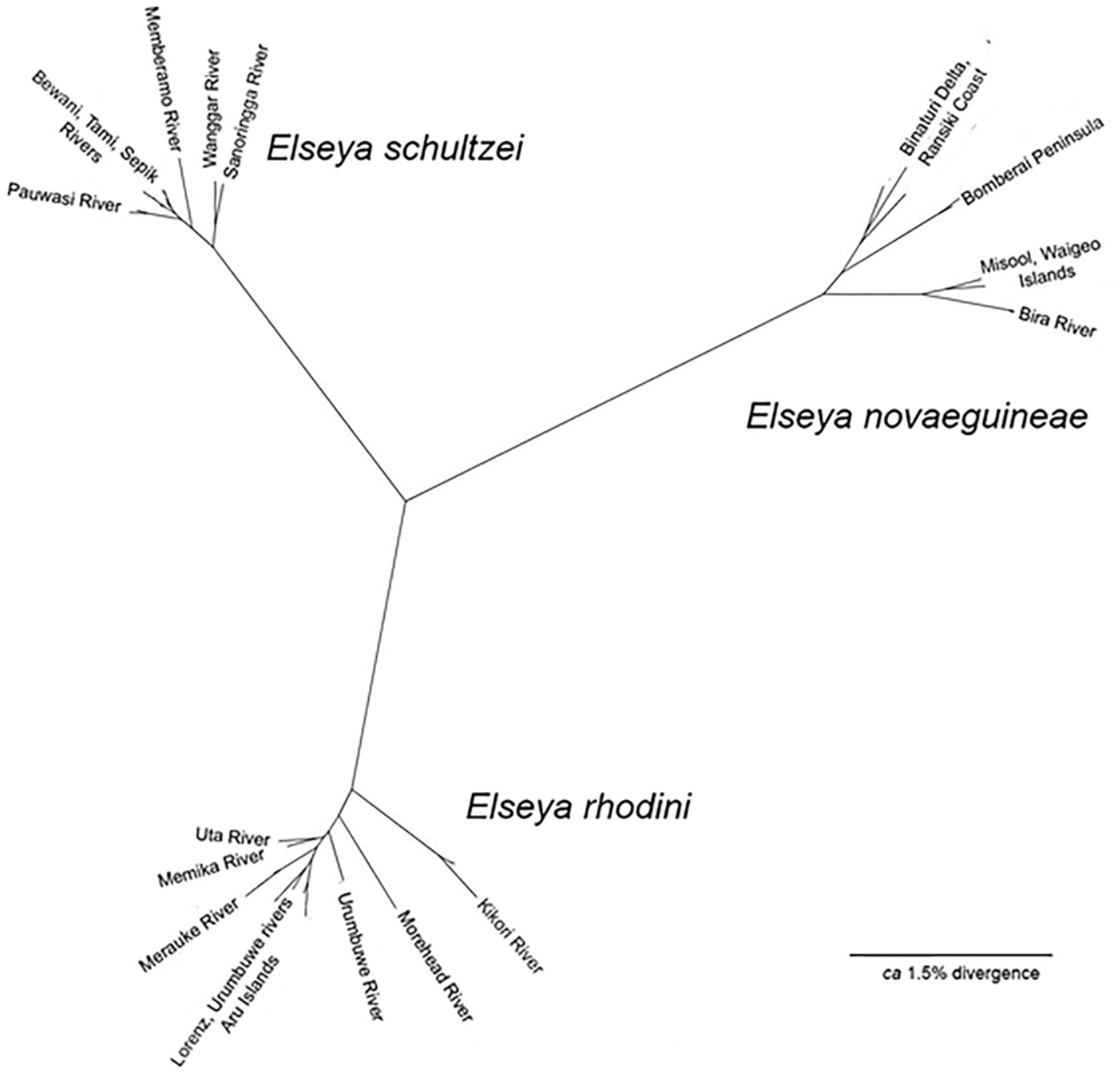

FIGURE 15. A neighbour-joining tree, based on mtDNA ND4 gene variation, summarizing the genetic distances between populations of *Elseya novaeguineae* from the Birds Head and associated islands of New Guinea, *E. schultzei* from north of the Central Ranges and *E. rhodini* from south of the Central Ranges and the islands of Aru. The scale is based on 1029 bp of coding mtDNA from ND4 and Cytochrome-b. Data from Georges et al. (2014).

Discussion

The three species of the subgenus *Hanwarachelys*, *Elseya novaeguineae*, *Elseya schultzei* and *Elseya rhodini*, each represent aggregations of lineages and minor clades that are allopatric. There are no localities at which two or more of these species are known to occur in sympatry. While morphological and genetic divergence are consistent with reproductive isolation, in cases of allopatry, it is an operational necessity to make judgments of species status on the basis of degree of differentiation (Georges & Thomson 2010). Our morphological analyses show diagnostic separation of the three taxa based on multivariate analysis of morphometric ratios, which complement the previously published genetic distinction between the three species. Georges et al. (2014) showed that aggregations of related populations to the north and south of the Central Ranges, and on Birds Head (Vogelkopf and Bomberai peninsulas), were deeply divergent, as divergent as each was from *Elseya branderhorsti*. For example, *Elseya*

rhodini, differs from *E. schultzei* at 6.2% of coding mitochondrial nucleotides and from *E. novaeguineae* at 7.3% of coding sites. This is comparable to its level of divergence from *E. branderhorsti* and well above the levels of divergence within these taxa (0.3–1.2%). The spectacular genetic divergence of the three taxa is shown in the data from Georges et al. (2014) reworked in a phenetic neighbor-joining analysis rescaled against nucleotide change in the coding ND4 and Cytochrome-b genes in Fig. 15. The genetic data complement and are qualitatively congruent with the morphometric analysis, that shows *Elseya rhodini* separated by a generalized distance of 29.4 units from *E. schultzei* and 141.4 units from *E. novaeguineae*. Together, these data corroborate, on the basis of degree of difference in allopatry (sensu Georges *et al.* 2002; Georges & Thomson 2010), our decision to split the *Elseya novaeguineae* species complex into three species using discrete qualitative characters.

Table 1. Selected measurements of the types of all species of the genus *Elseya*. Missing measurements are not preserved and hence cannot be measured in the relevant specimen. hl = head length; hwt = head width at tympanum; CL = carapace length (straight, midline); CW4 = carapace width at 4th / 5th peripheral (straight); CW8 = carapace width at 7th / 8th peripheral (straight); PL = plastron length (straight, midline).

Idno	Species	Status	hl	hwt	CL	CW4	CW8	PL
NHM 1947.3.6.2	*E. dentata*	Syntype	.	.	157.34	103.97	132.14	130.62
NHM 1947.3.6.3	*E. dentata*	Syntype	.	.	89.88	71.72	80.62	72.13
AM R72947	*E. dentata*	Referred	71.36	47.38	283.83	183.1	219.1	234.14
MTKD 8222	*E. novaeguineae*	Holotype	30.05	20.69	110.66	74.10	87.22	89.77
ZMB 22182	*E. schultzei*	Holotype	34.44	24.58	142.87	97.58	119.15	107.68
QM J59021	*E. irwini*	Paratype	28.75	20.82	103.62	66.44	92.39	80.79
QM J59431	*E. irwini*	Holotype	78.84	56.52	324.3	202.39	239.72	262.98
PNGM R25204	*E. rhodini*	Holotype	63.41	46.89	276.08	164.69	192.52	223.17
PNGM R25203	*E. rhodini*	Paratype	47.59	34.33	202.05	135.17	150.18	169.87
QM J81785	*E. albagula*	Holotype	96.1	69.22	382.4	263.73	299.33	315.4
QM J28449	*E. albagula*	Allotype	67.52	53.08	275.49	182.7	214.77	224.87
QM F24121	*E. lavarackorum*	Holotype	--	--	--	--	--	370
QM J47911	*E. lavarackorum*	Referred	58.62	42.15	254.93	168.24	190.13	199.92
PNGM R25201	*E. branderhorsti*	Neotype	71.85	53.86	424.70	252.58	302.76	372.22
QM J93362	*Elseya* sp.	Referred	66.76	49.76	300.48	192.96	224.38	245.97
QM J23300	*Elseya* sp.	Referred	80.89	60.41	346.63	222.49	248.54	271.41
NTM 13512	*Elseya* sp.	Referred	67.75	47.48	311.5	189.94	224.65	269.26

By splitting up the *Elseya novaeguineae* species complex, we resolve long-standing references to the existence of more than one species in the taxon until now referred to as *Elseya novaeguineae*. Our analyses, and those of Georges *et al.,* (2014), do not however support the existence of a single species to the north and two species to the south (Iskandar 2000; Rhodin & Genorupa 2000), nor do they support the plethora of potential species in northwestern Vogelkopf near Sorong, in the Sepik River, on the island of Waegeo, or on the Islands of Aru (Rhodin

& Genorupa 2000). The status of the population in the wetlands of the highland plains of Mt Jayawijaya (Iskandar 2000) remains an open question, as material from this population was not available to us.

The genus *Elseya* has been problematic taxonomically (reviewed by Georges & Thomson 2010). Instances of paraphyly led to suggestions that it be synonymized with the genus *Emydura* (Gaffney 1981; McDowell 1983), but this did not gain wide acceptance (Legler & Cann 1980; Georges & Adams 1992). Instead the paraphyly was resolved by the creation of a new genus, *Myuchelys* to which *Elseya latisternum* and related species were assigned (Thomson and Georges, 2009). This genus was not erected on synapomorphy, but rather on the basis of a suite of shared ancestral characters, which presents inevitable difficulties in assigning new species to it. On the basis of a suite of shared primitive characters—presence of a cervical scute, absence of an alveolar ridge on the trituration surfaces, a narrow parietal arch and head shield extending down the side of the head toward the tympanum—Georges and Thomson (2010) tentatively placed *Elseya novaeguineae* in the genus *Myuchelys*, pending more detailed sequence analyses. They acknowledged that DNA analyses that included *E. schultzei* (as conceived here) placed it clearly in *Elseya,* not *Myuchelys*.

In addition to describing a new species, we take into account recently published evidence to clarify this issue and define three new subgenera representing the three major clades of *Elseya*. This nomenclatural refinement will better define groups of taxa that have been previously referred to as the ill-defined Queensland *Elseya*, the northern Australian *Elseya* and the New Guinea *Elseya*, in the same way that definition of subgenera in *Chelodina* clarified the prior terminology of Group A, B and C taxa (sensu Burbidge *et al.* 1974) or Group A and B taxa (Legler 1981). *Elseya novaeguineae*, *E. schultzei* and *E. rhodini* belong to a different subgenus (*Hanwarachelys*) than *E. branderhorsti* (*Elseya*). The relationships among the three subgenera remain unresolved and require further investigation.

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APPENDIX A. Specimens Examined.

Abbreviations used: AM, Australian Museum; AMNH, American Museum of Natural History, New York; ANWC, National Wildlife Collection; NHM, Natural History Museum of London; MTD, Museum für Tierkunde, Senckenberg Dresden; ZMB, Museum für Naturkunde Berlin, MV, Museum of Victoria; NTM, Museums and Art Galleries of the Northern Territory; PNGM, Papua New Guinea National Museum; QM, Queensland Museum; RMNH, Nationaal Natuurhistorisch Museum, Leiden; UU, University of Utah collection of J.M. Legler; WAM, Western Australian Museum; UC, University of Canberra collection of the senior author; NT, Northern Territory; WA, Western Australia; QLD, Queensland; NSW, New South Wales.

Elseya (Elseya) branderhorsti: PNGM R25201-02, Bensbach River of the Trans-Fly region of Papua New Guinea (8° 50' 58.6896" S., 141° 14' 52.944" E.)

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

(14°18'S, 132°25'E); UU 14839 Ferguson River, 23 mi N, 18 mi W of Katherine (14°04'S, 131°58'E); NTM 2973 Daly River (14°41'S, 131°34'E). Darwin Region—NTM 7058 Casuarina (12°23'S, 130°54'E); NTM 34498 Darwin (12°27'S, 130°50'E); NTM 34497 Howard Springs (12°27'S, 131°03'E); NTM 21922 Sandy Creek, Litchfield National Park (13°16'S, 130°44'E); UU 14776 Finnis R. (35 mi S Darwin) (13°04'S, 130°58'E); NTM 21717 Tjaynara Falls, Litchfield National Park (13°15'S, 130°44'E); UU 14774–5 Adelaide Drainage, 60 mi S, 12 mi E Darwin (12°34'S, 131°24'E). Alligator Rivers Region—UU 14784–92 Barramundie Creek 3 mi S, 7 mi W Spring Peak (13°01'S, 132°23'E).

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

Elseya (Hanwarachelys) novaeguineae: MTD D8222 from Passim, Barbussi River, ca. 3 km N. Sieb, 1 km S. Tandjung Sjeri (= Syeri), west shore Geelvink Bay (= Cenderawasih Bay), Papua, Indonesia (1˚41'S,134˚05'E) MTKD8222 RMNH27949 RMNH27955 RMNH27956 RMNH27968

Elseya (Hanwarachelys) rhodini: PNGM R25203-04 Rue Creek (tributary of Wau Creek), Gulf Province, Papua New Guinea (07˚11' 67.3" S, 144˚37' 13.8" E) MCZ134421 MCZ134422 MCZ134423 MCZ134424 MCZ134425 MCZ134426 MCZ134429 MCZ134430 MCZ134431

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

Elseya (Pelocomastes) albagula: Fitzroy-Dawson Drainage.—UU 17898–903 Connors River 3.5 km W, 3.0 km S, Connors River (22°13'S, 149°01'E); QM 48615 Belmont Creek, Fitzroy River (23°16'S, 150°28'E); QM 37933 Dawson River Crossing, at Baroondah Station (25°41'S, 149°13'E); QM 47987, 47998, 48002, 48010, 48039 Dawson River, Theodore (24°57'S, 150°05'E); QM 28449 Emerald, Nogoa River, Town Weir (23°31'S, 148°01'E); UU 17096–102 Fitzroy River 63 km N, 25 km E Duaringa (23°11'S, 149°55'E); QM 38533 Rockhampton, lagoon 18 km W (23°17'S, 150°25'E); UU 17093–5, 17274 Raglan Creek 12.5 km W and 1.5 km N Mt. Larcom (23°49'S, 150°52'E); UU 17874–81, 17888–97 Raglan Creek 3.7 km E, 8.5 km S Raglan (23°48'S, 150°51'E); AM 129338–40, QM 59269 Raglan Creek, nr. Raglan (23°38'S, 150°49'E); UU 17882–7 Raglan Creek, 5.5 km W, 9.3 km S Raglan (23°48'S, 150°46'E). Burnett River—QM J81785, 59270 Walla Weir, Burnett River (25°03'S, 152°05'E); UU 17086–92 Barambah Creek 7.8 km S, 9.2 km E Gayndah (25°41'S, 150°48'E); UU 14872 Barambah Creek 3.2 mi E, 2.8 mi N Gayndah (25°35'S, 151°40'E); QM 48026 Burnett River, Grays Waterhole, nr. Gayndah (25°37'S, 151°37'E); QM 48029, 48052 Burnett River, Jones Weir (25°36'S, 151°18'E); QM 48027 Burnett River, Munduberra (25°35'S, 151°18'E); QM 48012, 48046 Burnett River, nr. Gayndah (25°37'S, 151°37'E); QM 2966, AM 6110, Eidsvold (25°22'S, 151°07'E); NHM 75.5.4.8, 76.5.19.77, 1875.5.4.7–8, QM 4501, 4505 Gayndah (25°37'S, 151°37'E); AM 123067 Grey's Waterhole, Burnett River (25°32'S, 151°39'E). Mary River—UC 0305–6 Mary River; QM 36036, 36042, 36045 Tuan State Forest, Tinana Creek, Missings Bridge (25°41'S, 152°53'E); QM 36039, 36041, 36044, 36046–7, 59271 Coondoo Creek, Tin Can Bay Road (25°59'S, 152°50'E).

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

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

Elseya* (*Pelocomastes*) sp. aff. *lavarackorum (Johnstone) (Voucher Label, Georges and Adams, 1992): Cairns District.—AM 68848, 93048 Cairns district (168550S, 1458460E); QM 48062, 48068 Hartley Creek (158460S, 1458190E); AM 125468, QM 23053–4, 23056–7, 23060, 23175–6, 23299–300, 23322, 28954, UU 14845–71 Malanda, North Johnstone River (178210S, 1458350E); QM 48060 nr. Cairns (168550S, 1458460E); QM 48059, 48064–5 South Johnstone River (178380S, 1458050E)

Elseya* (*Pelocomastes*) sp. aff. *lavarackorum QM J93356-7 Upper Daintree River, Queensland, (-16.30601, 145.15051); QM J93358-9, Boolbun Creek, Daintree National Park, Queensland, (16.06833S, 145.15454E); QM J93360-61 (Daintree) Daintree River, Daintree National Park, Queensland, Australia (-16.16591S; 145.26842E); QM J 93362 Douglas creek, Daintree National Park, Queensland, Australia (-16.28547S; 145. 27285E).