Inframarginal Scutation in Australasian Chelid Turtles (Testudines: Chelidae)

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ABSTRACT. – Numerous fossil Mesozoic and Cenozoic turtle taxa of the cryptodiran lineages, including Paracryptodira and Eucryptodira, are characterized by series of inframarginal scutation of the lateral plastron. In extant representatives of the subordinal turtle lineages, inframarginal scutes are again most marked in cryptodires among which some retain full series of inframarginals, including sea turtles of the family Cheloniidae, the riverine Dermatemyidae and the semi-terrestrial Platysternidae. Amongst these scutes, two occur in the form of axillary and inguinal scutes at the polar ends of the bridge, which may be reduced in the freshwater families Geoemydidae and Emydidae, and terrestrial Testudinidae. In pleurodires, these two scutes are only present in several genera in both South American and Australasian chelid turtles but are mostly extremely reduced in size. With the exception of a few brief mentions in the published literature on the chelids of Australia and New Guinea, no formal documentation of the presence of axillary and inguinal scutes, or illustrations of these exist, nor any record of which taxa possess them. They are most likely overlooked in descriptions because their positions on the plastral bridges are normally associated with Rathke's gland (the musk glands). We examined specimens of all extant Australasian taxa and, for the first time, provide an account of those that typically do and do not possess axillary and inguinal scutation, along with illustrations and descriptions of shape, relative size and plastral positioning of them. These scutes may be applicable as diagnostic characters for some taxa.

Keywords: Testudines; Chelidae; Axillary; Inguinal; Australia; New Guinea; Indonesia.

Joseph-Ouni, M., Cann, J. & McCord, W.P. 2025. Infarmarginal scutation in Australasian chelid turtles (Testudines: Chelidae). *Chelonological Contributions* 2: 24 pp. http://doi.org/10.70661/ChelContribjtbb6388201582

Published January 16, 2025
Special Series Editor: Anthony Pierlioni

The Official Science Journal of theTurtleRoom
theturtleroom.org

Chelonological Contributions ISSN: 3065-3290
DOI: 10.70661/ChelContribjtbb6388201582

Figure 1. *Elseya dentata,* a northern Australian species with the largest inframarginal scutation amongst Australasian chelids.

INTRODUCTION

Multitudinous taxa amongst diverse extinct turtle families throughout the Mesozoic and Cenozoic, and fossil species of some extant families, are characterized by a series of keratinous scutes on the plastron located along the bridge which comprise the term inframarginal scutation. Fossil species of the Paracryptodira and Eucryptodira clades also possessed complete series of large inframarginal scutes (Baenidae, for example, Joyce & Lyson, 2015) illustrating that this character state was basal to the Testudines order and widespread but subsequently largely reduced or lost entirely in the course of evolution of the scutation of the modern turtle bridge.

In living Cryptodires, inframarginal scutes are prominent in all members of the sea turtle family Cheloniidae, and in the monotypic riverine family Dermatemydidae of Central America, and large but less ostentatious in the freshwater Chelydridae and semi-terrestrial Platysternidae. The freshwater and terrestrial families Geoemydidae and Emydidae, and the terrestrial Testudinidae, lack a series of medial bridge inframarginals but possess scutes at the polar ends of the bridge. These scutes are generally reduced and confined to the anterior bridge in the form of the axillary scute and the posterior bridge in the form of the inguinal scute.

In living Pleurodires, axillary and/or inguinal scutes exist in two of the three extant lineages - absent in the Podocnemididae, relatively moderate in size in the Chelidae and vestigial or aberrant in some select Pelomedusidae. These scutes are generally very reduced and restricted in both South American and Australasian members of the family Chelidae and even then occur only in some genera. They have been almost routinely overlooked in the literature possibly because their positions on the plastron are normally associated with the external pores of Rathke's glands (musk ducts) and, due to their small size when present, care is required to discern that they bear distinct lamina with distinct sulci.

As a consequence, only a few brief mentions of these scutes exist in the published literature on chelid taxonomy and morphology of Australasian turtles (e. g. Thomson *et al.* 2006; Joseph-Ouni & McCord, 2019a,b; Joseph-Ouni *et al.*, 2020), and with those exceptions, no formal documentation of the presence of the scutes, descriptions nor illustrations exist, nor does a formal record of which genera and species possess them.

To rectify this situation, we examined living and museum specimens of all extant chelid species from Australia, New Guinea, Solomon Islands, Indonesia and Timor Leste and, for the first time provide illustrations and descriptions of the shape, relative size and plastral positioning of these axillary and inguinal scutes, and propose that these scutes may be a diagnostic character for some taxa.

METHODOLOGY

Specimens and / or photographs of *Chelodina* (all three subgenera *Chelodina, Macrochelodina, Chelydera*); *Elseya* (all four subgenera *Elseya, Hanwarachelys, 'Pelocomastes', Solomonemys*), *Emydura, Pseudemydura, Elusor, Wollumbinia*, and

Rheodytes in the Queensland Museum (QM); Museums and Art Galleries of the Northern Territory (NTM); Australian Museum (AMS); Natural History Museum, United Kingdom (NHMUK); Museum of Victoria (NMV); Yale Peabody Museum (YPM); American Museum of Natural History (AMNH); Museum of Comparative Zoology (MCZ) and living specimens of these genera were examined physically or from high-quality photography to compile data on the presence of axillary and inguinal scutes.

Nomenclature of the plastral scutes follows that of Zangerl (1969).

We are unaware of and were unable to locate a specific and/ or formal description of the structure or defining characters of axillary and inguinal scutes in extant Testudines, although their locations are illustrated by Zangerl (1969). For the taxa discussed here we use the following nomenclature of the inframarginals to consist of the following: The anterior-most scute that covers the bridge anterior of the axillary notch located between the pectoral and marginal scutes is referred to as the *axillary scute*. Where present, it usually encapsulates the external pore of Rathke's gland. The posterior-most scute that covers the bridge posterior of the inguinal notch and located between the bridge femoral scutes and the marginal is referred to as the *inguinal scute*. It also usually encapsulates the external pore of Rathke's gland.

In non-chelid species in which there are additional scutes covering the bridge located at and between the axillary and inguinal notches (i.e. chelonid sea turtles, platysternids) the scutes are referred to here as *mesomarginal scutes*. Hence the axillary, inguinal and mesomarginals scutes collectively comprise the inframarginal scutation.

With regard to the relative sizes of axillary and inguinal scutes we consider two size classes: 'large' to represent a scute that is at least half as long or longer than an adjacent marginal; 'small' is considered less than half the length of an adjacent marginal. Scutes that were one-fifth or less in total length of the adjacent marginal usually simply enclosed the external pore of Rathke's gland with minimal circumferential keratinous laminae. These latter scutes were considered vestigial in nature and were noted but not described further.

These scutes may be considered diagnostic when they are of a consistent shape and when they are present in the majority of specimens of a taxon.

The polar areas of the bridge that were absent of any keratinous axillary or inguinal scutes simply contain soft tissue (ie. *Chelodina*).

We do not take a position regarding nomenclature of the *Elseya* from the northeastern Northern Territory named by Wells (2002; 2007) as *E. jukesi* and renamed by Thomson & Georges (2016) as *E. flaviventralis* (the latter authors holding the view that *E. jukesi* is a nomen nudum; also see Cogger *et al.,* 2017 for discussion of this nomenclatural issue). For the purposes of this paper, we refer to the taxon simply as *E. jukesi/flaviventralis*; we note however that the nomen *E. flaviventralis* is now in prevailing use in the literature.

RESULTS

A summary of results is presented in the Appendix for each taxon. Figures (2-18) show the condition (presence or absence) of any axillary or inguinal scutes considered as a typical character state for a taxon, or their atypical presence.

None of the taxa currently recognized for the genus *Chelodina* (all three subgenera, n = 3 per species, except 1 for *C. kuchlingi*) possessed either axillary or inguinal scutes, only the pores of Rathke's glands opening through adjacent skin, and it can be confidently stated that these scutes do not occur in *Chelodina* (Figure 2). The anterior-most point of the hyoplastral bridge makes full contact with the respective marginal. Likewise, the posterior-most point of the hypoplastral bridge makes full contact with the respective marginal. The single observed exception was an axillary and inguinal set of scutes in a large female specimen of *C. novaeguineae* (MCZ 53758 – Figure 2) which was collected at the junction of the Fly and Strickland rivers, but the scute set is clearly an abnormality as occurs frequently and widely in turtles (Pritchard, 2008).

In *Emydura* (n = 3 per species or subspecies) no taxon consistently possessed either axillary or inguinal scutes, although reduced, small axillaries were present in several specimens (Figures 2, 3) but considered as atypical variation or minor vestiges because the majority of specimens lacked them entirely. Several of the holotypes of the eastern *Emydu-*

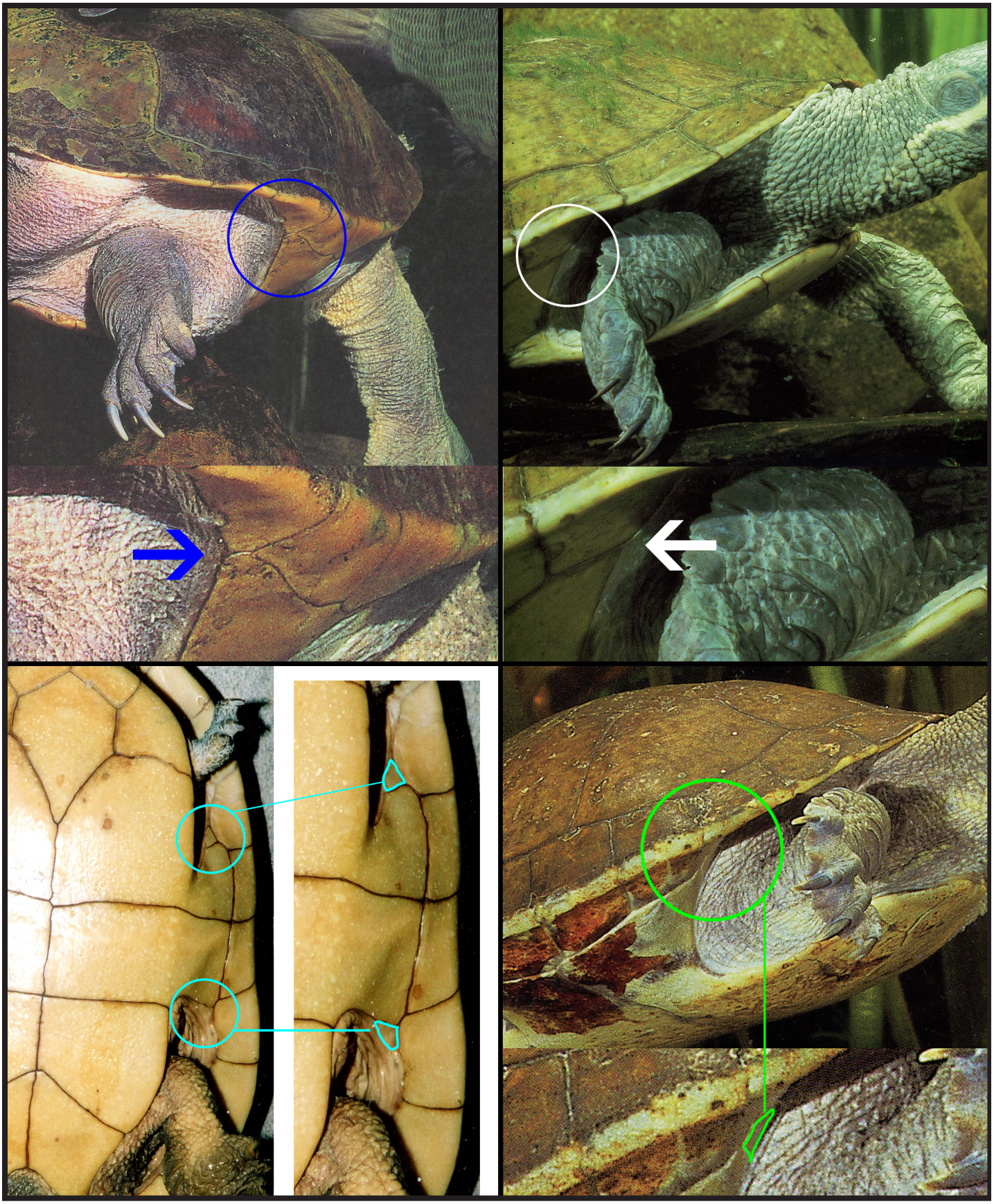

Figure 2. Axillary and inguinal scutation as absent in *Chelodina* (top left, live *C. rugosa*) and *Emydura* (top right, live *E. macquarri signata*), and in the single instance in a long-necked specimen (*C. novaeguineae*, bottom left, MCZ 53758) and as an atypical variant in *Emydura* (*E. worrelli,* bottom right, live).

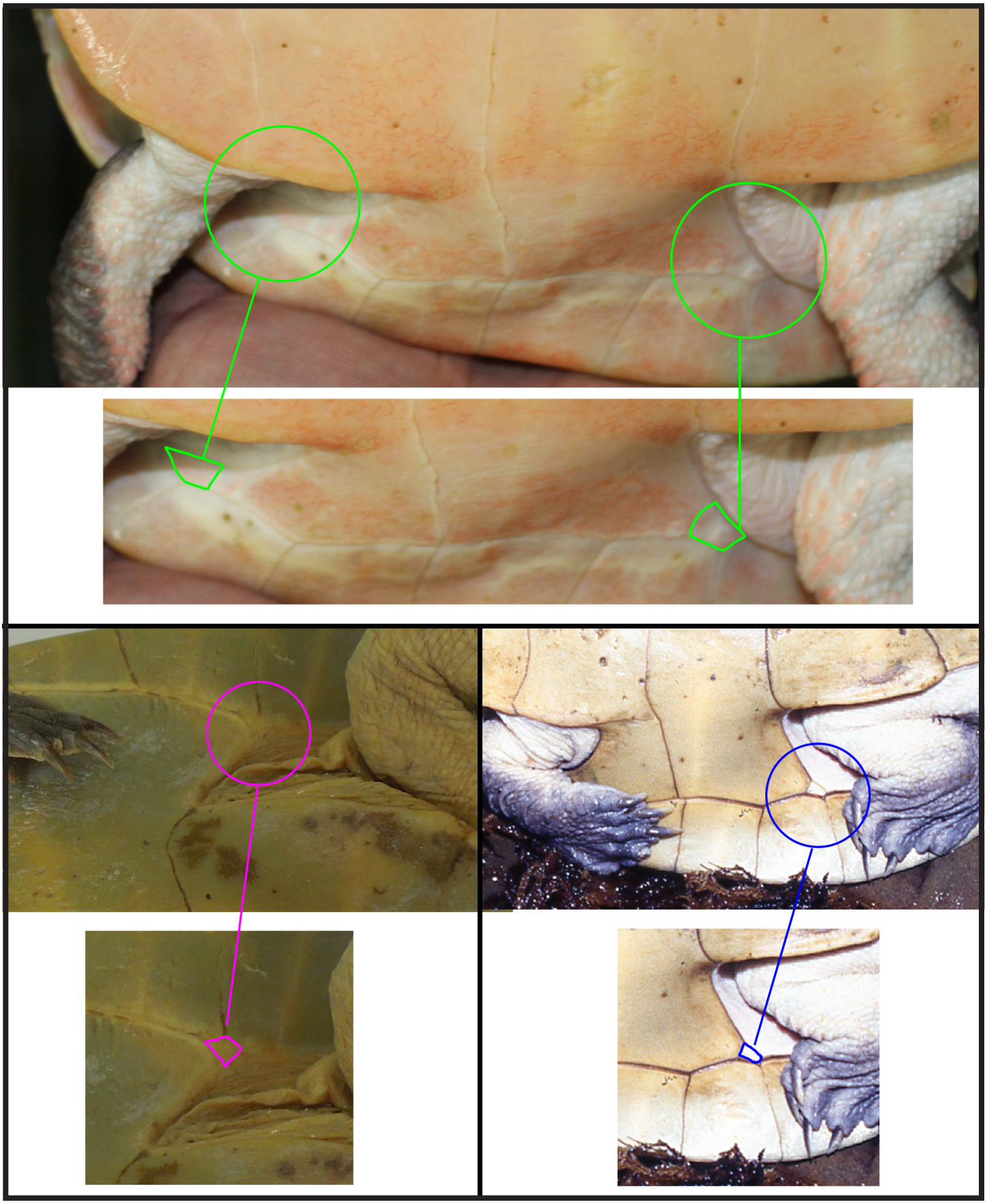

Figure 3. *Emydura*: Atypical axillary and/or inguinal scutation in *E. subglobosa subglobosa* top (live); infrequent state of inguinal area in *E. australis*, bottom left (AM R136093, male) and *E. victoriae* bottom right (live male).

Figure 4. Ilustrations of axillary and/or inguinal scutation, when present, in the *Elseya* subgenus '*Pelocomastes*', left side (*E. albagula* holotype QM J81785) and *Wollumbinia*, right side (*W. purvisi*, live).

ra macquarii subspecies (*E. m. binjing, E. m. dharuk, E. m. gunabarra*) possess small inguinal scutes only but these were inconsistent in the larger series. In *Emydura* and *Wollumbinia* (n = 3 per species) the position at the posterior-most point of the hypoplastral bridge ends in a small demarcation that simply accommodates the external pore of Rathke's gland, although sometimes this was larger but again considered atypical as they were absent in the larger series (Figure 4).

In *Pseudemydura* (n = 3), no specimen examined displayed either axillary or inguinal scutes, only the pores of Rathke's glands opening through adjacent skin. However, as only digital photography of a small pool of specimens was available to us, we recommend researchers with access to physical specimens further evaluate this observation.

In *Elusor* (n = 4), both scutes were present. The axillary scute occurs as an elongated but very thin figure (shaped anterior to posterior) that shares a common sulcus with marginal 4 from its anterior-most interior point to the approximate posterior-third point of the marginal 4 sulcus (Figure 6). The inguinal scute is an asymmetrical polygonal with a long side marking the skin boundary of the hypoplastron and opposing sides sharing a common sulcus with the posterior-most marginal 7 and anterior-most third of marginal 8.

In *Rheodytes* (n = 4) both scutes are present (Figure 7). The axillary scute is relatively large (larger than the inguinal) and well-defined. It approximates an equilateral triangle that makes contact and shares a common sulcus with the posterior-most third of marginal 3 and extends to the middle marginal 4. The inguinal approximates an isosceles triangle, with one long side bordering the skin portion of the hypoplastron and the other long side sharing a common sulcus with almost the full length of marginal 7.

In *Elseya* subgenus *'Pelocomastes'* (n = 3 per species), axillary and inguinal scutes were sometimes present but as extremely reduced elements (in most cases the inguinal scute area simply accommodating the pore of Rathke's gland)

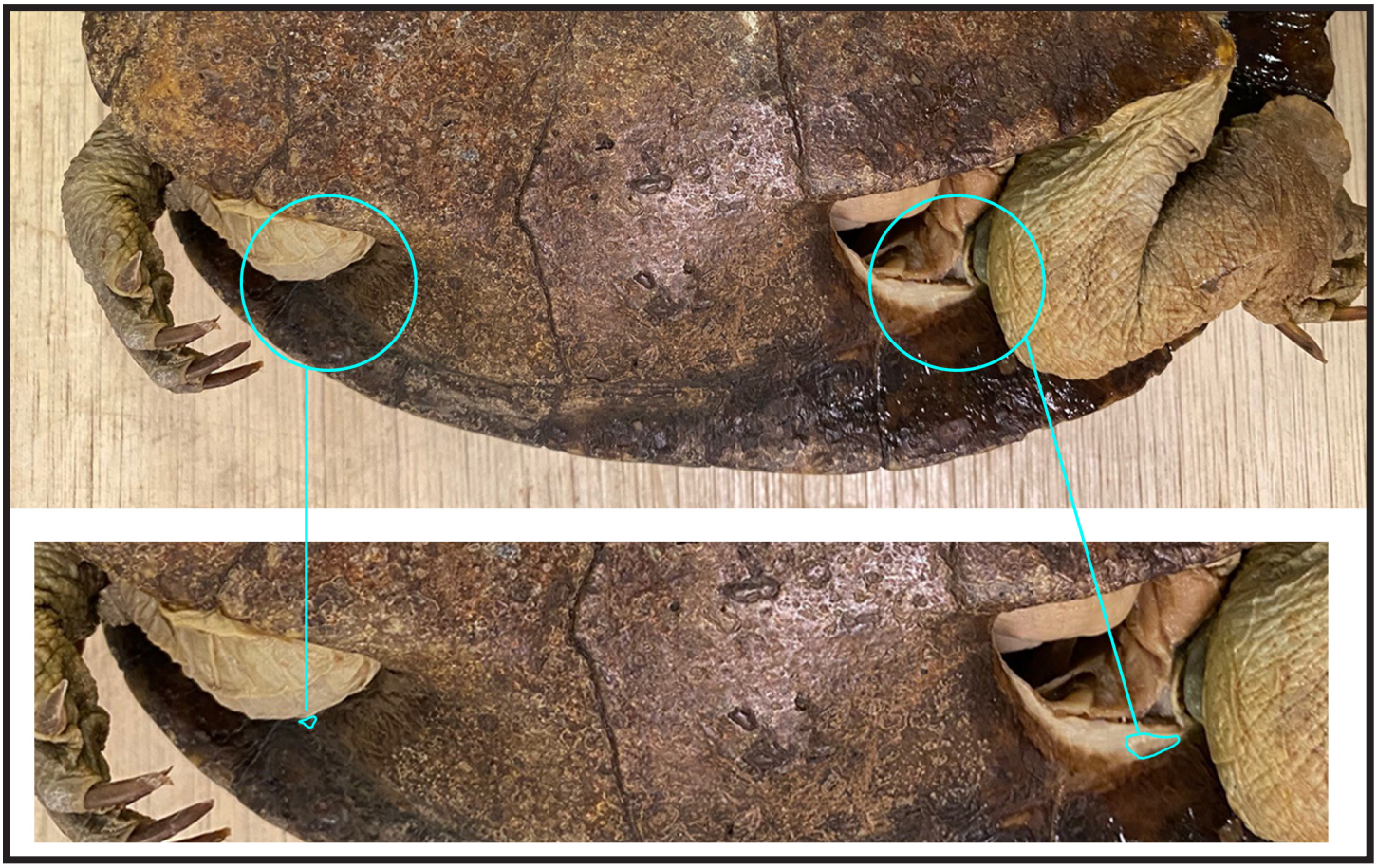

Figure 5. Irregular axillary and inguinal scutation in *E. 'P') gondwana* (female holotype), a species only recently formally described but originally discovered by J. Cann in the Roper River in the early 1980s.

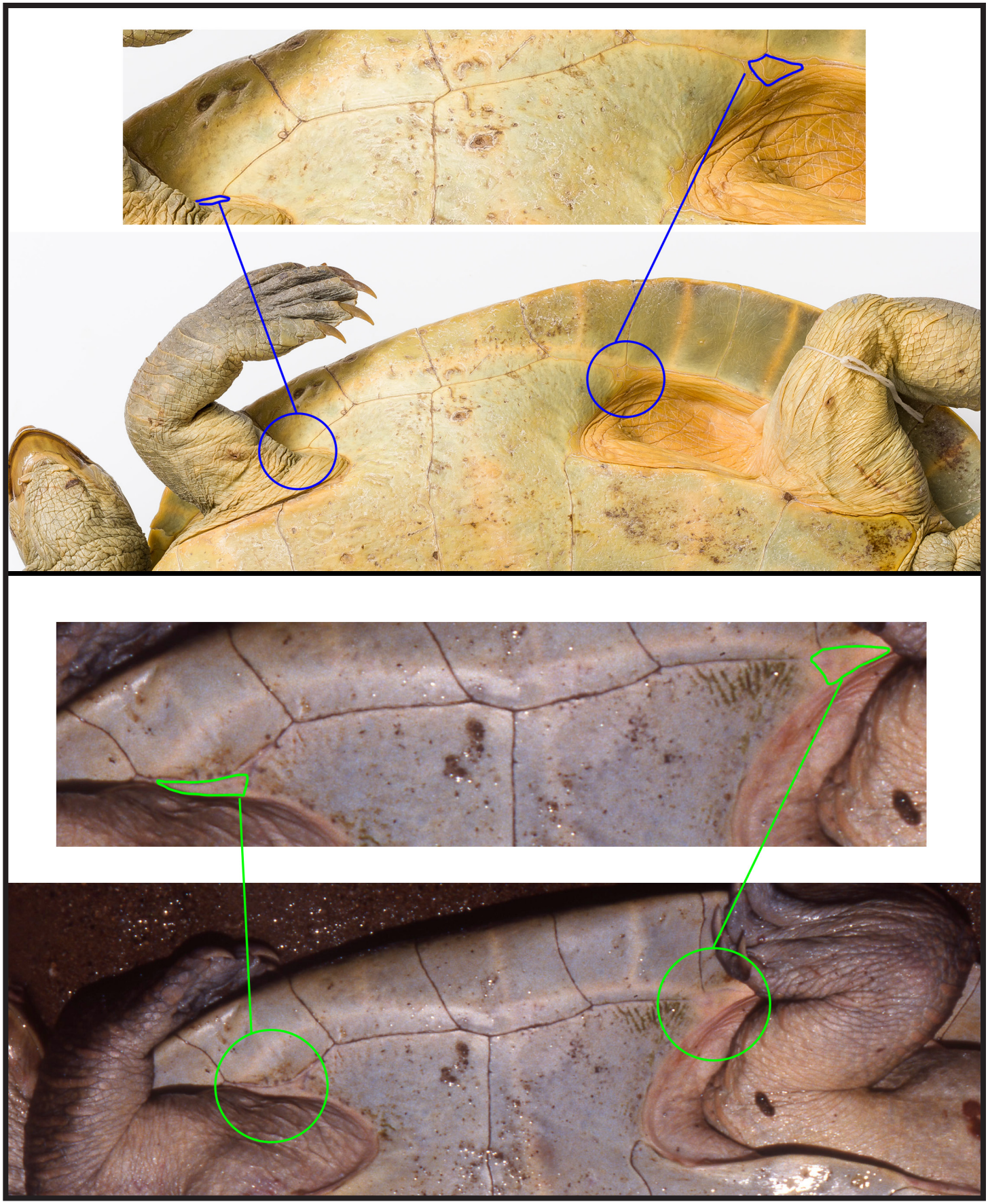

Figure 6. Axillary and inguinal scutation in typical *Elusor macrurus* top (holotype female QMJ51275) and bottom (live male).

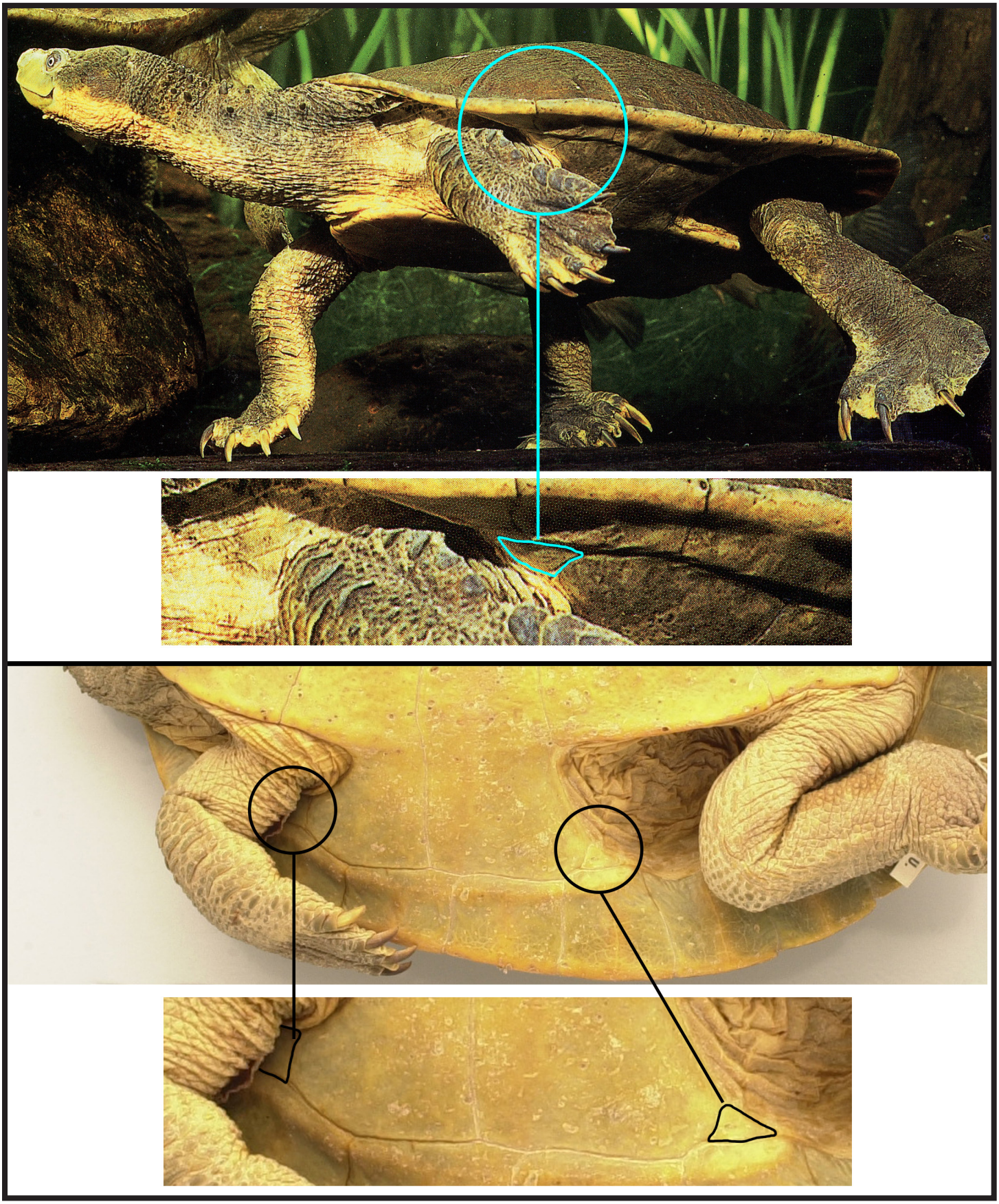

Figure 7. Axillary and inguinal scutes in typical *Rheodytes leukops* (axillary scute, above, live male) and (bottom, female holotype QMJ31701).

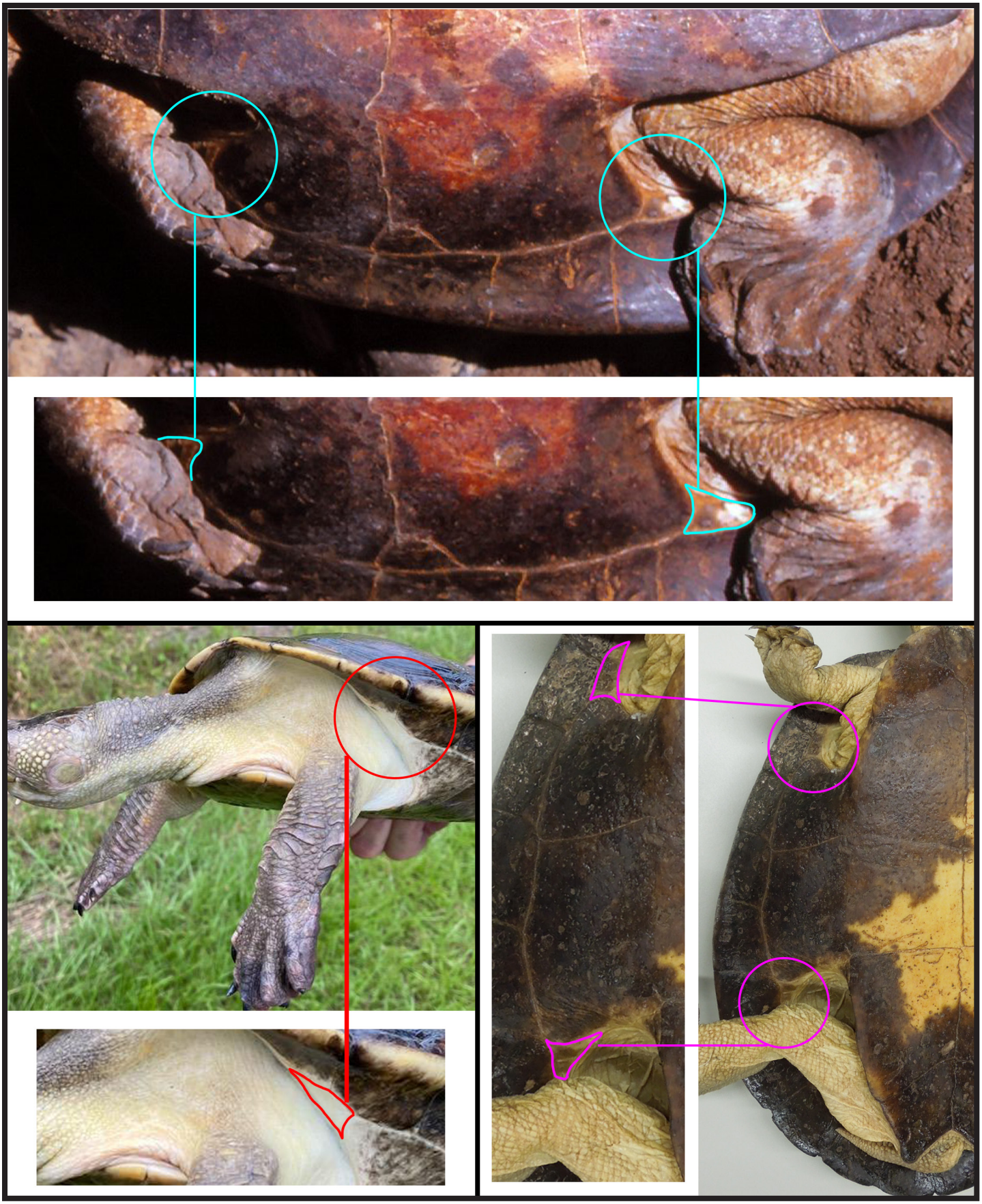

Figure 8. Axillary and inguinal scutation in *Elseya (Elseya) dentata*: top - live female, Bullo River; bottom left - live male, Daly River; bottom right, female, AM R72936, Bullo River.

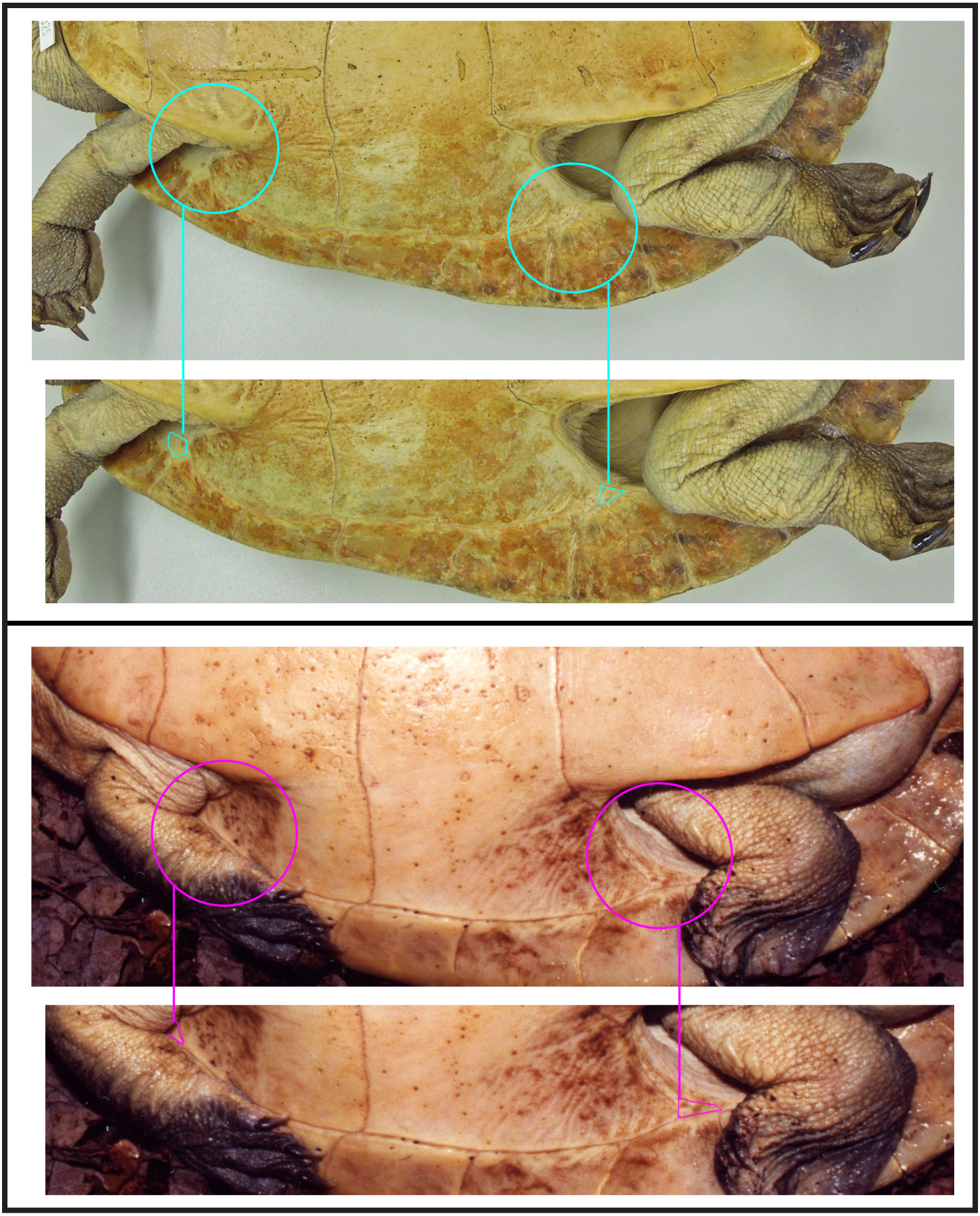

Figure 9. Axillary and inguinal scutation in *Elseya (Elseya)* continued: *E. jukesi*/ *flaviventralis* (top, female, Brockman Range, Northern Territory - AM R38325); *E. branderhorsti* (bottom, live female, Merauke, Indonesia).

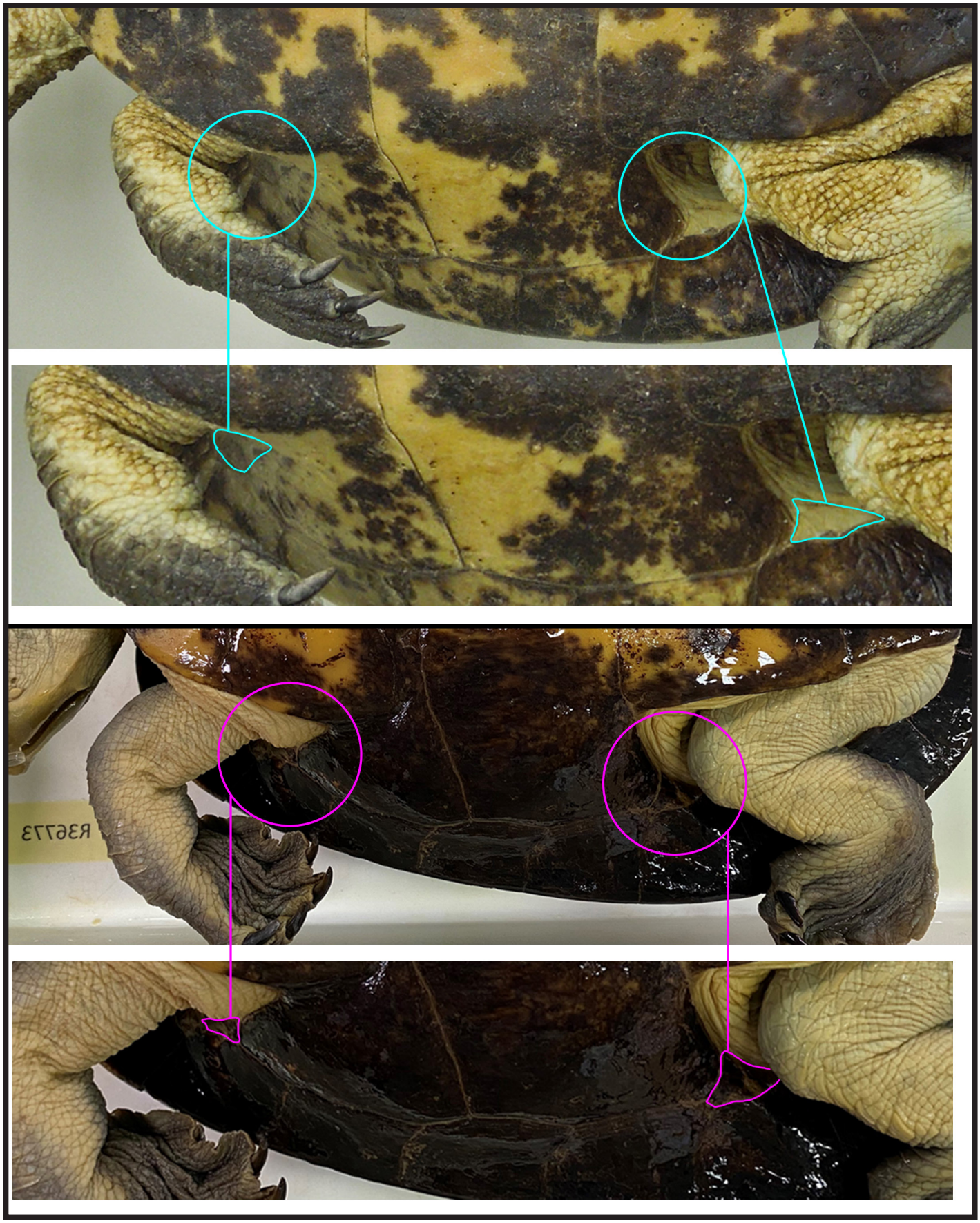

Figure 10. Axillary and inguinal scutation in *Elseya (Elseya)* continued: *E. kalumburu* (top, female paratype AM R183181 Carson River, Western Australia); *E. sahul* (bottom, NTM R36773, holotype, Roper River, Northern Territory, Australia).

Figure 11. Inguinal scute (magenta triangle) as seen in the only known live specimen of *Elseya (Elseya) lavarackorum*, serendipitously photographed by Les McKenzie in September, 1979 during a family camping expedition along the Nicholson-Gregory drainage in northwestern Queensland. The axillary scute, if present, is unfortunately concealed under the forelimb.

or entirely absent. Both were present in several specimens but considered as variants, and hence not species-specific. When present, the axillary or inguinal scute was relatively large (as in the holotype of *E. (P.) albagula* (Figure 4) but they were not consistently present in all specimens examined). In the newly described species of *E. (P.) gondwana* (Figure 5), the scutes are present in some specimens but follow the same overall inconsistent pattern.

The *Elseya* subgenus *Elseya* consistently displayed well-defined (strongly delineated sulcus), and in relative terms, the largest axillary and inguinal scutes of all the taxa investigated, the largest being seen especially in *E. (E.) dentata* (Figures 1, 8), a widespread species in northern Australia (Figure 19).

In *E. (E.) dentata* (n = 10) the axillary approximates an elongated polygon, with the longest side in contact for its full length from the posterior third of marginal 3 to the middle of marginal 4 (Figure 8). The inguinal approximates an isosceles triangle with one of the long sides bordering the hypoplastral skin and the other long side in contact for its length from the anterior or anterior first third of marginal 8 to posterior marginal 8.

In *E. (E.) jukesi/ flaviventralis* (n = 4), the axillary approximates a shortened polygon, with the longest side in contact for its full length from the posterior third of marginal 3 to the anterior quarter of marginal 4 (Figure 9). The inguinal approximates an elongated triangle with the hypotenuse bordering the hypoplastral skin and a shorter side in contact for its length from the anterior to middle marginal 8.

In *E. (E.) branderhorsti* (n = 8), the axillary was not regularly present. When present it approximates a small triangle with one side in contact for its full length anterior to middle marginal 4 (Figure 9) but could range to a large triangular scute. The inguinal is present but normally small (smallest of the subgenus) and varies from an equilateral triangle to an isosceles triangle, one side in contact for its length from the middle to posterior quarter of marginal 8.

In *E. (E.) sahul* (n = 3) the axillary approximates a large, unequal polygon, with a short side in contact for its full length from the posterior third of marginal 3 and one long side sharing the anterior third of marginal 4 (Figure 10). The inguinal is very large and approximates an unequal polygon with the shortest side sharing the mid-anterior marginal 7 sulcus and the longest side in contact for its length from the anterior or anterior first third of marginal 7 to posterior marginal 8. The condition of these scutes when present in the species, *E. (P.) gondwana,* with which it is sympatric in the Roper River, is shown in Figure 5 for comparison.

In *E. (E.) kalumburu* (n = 3) the axillary approximates an elongated rounded polygon, with the longest side in contact for its full length from the posterior third of marginal 3 to the middle of marginal 4 (Figure 10). The inguinal is very large and approximates an unequal polygon with one side in contact for its length from the anterior or anterior first third of marginal 8 to anterior marginal 9.

In *E. (E.) lavarackorum* (n = 1), the axillary scute is currently undetermined; the inguinal scute is a small triangle located at middle marginal 8 (Figure 11).

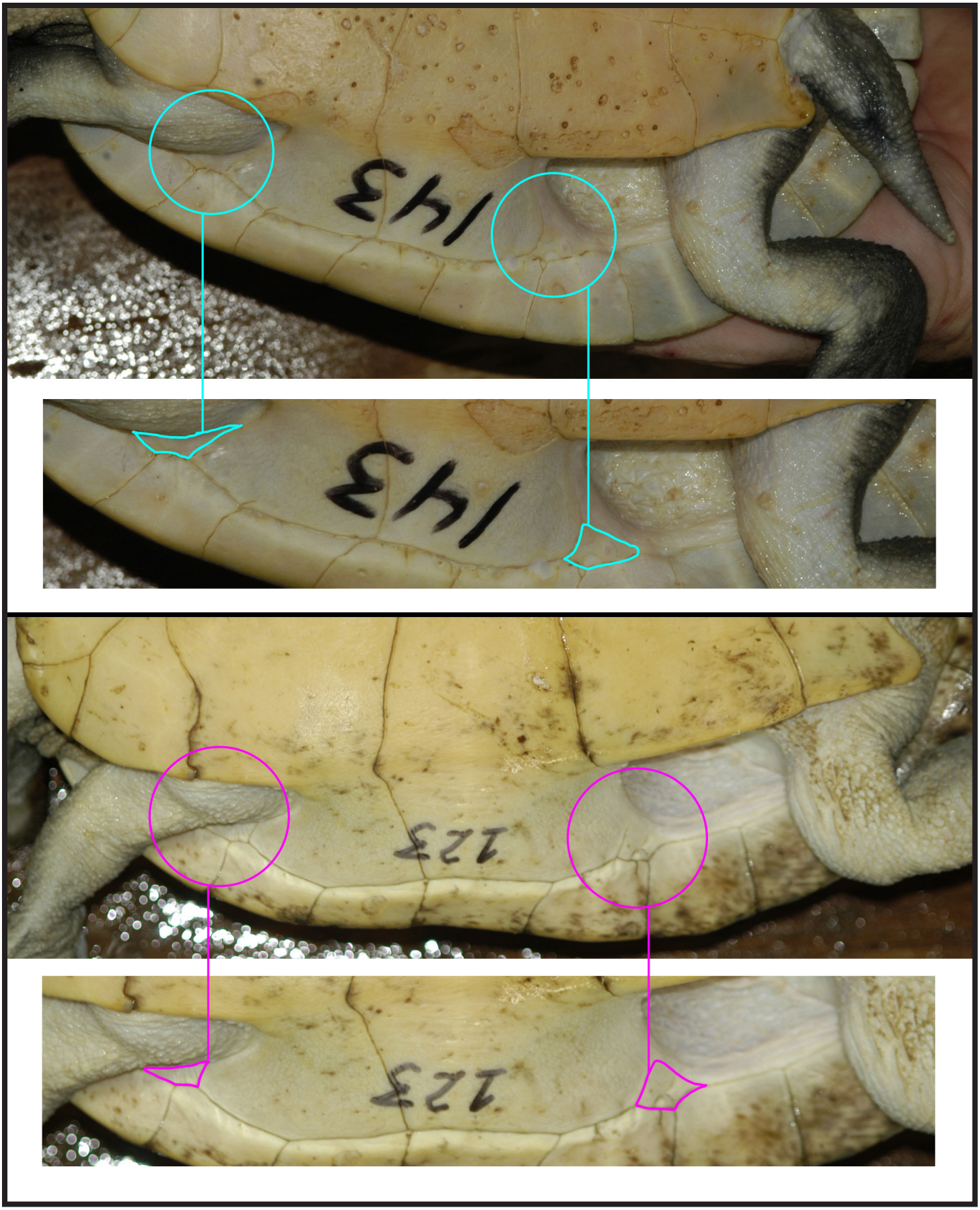

Figure 12. Axillary and inguinal scutation in *Elseya (Hanwarachelys)*: *E. novaeguineae* (top - Bintuni); *E. schultzei* (bottom, Tami River), both live.

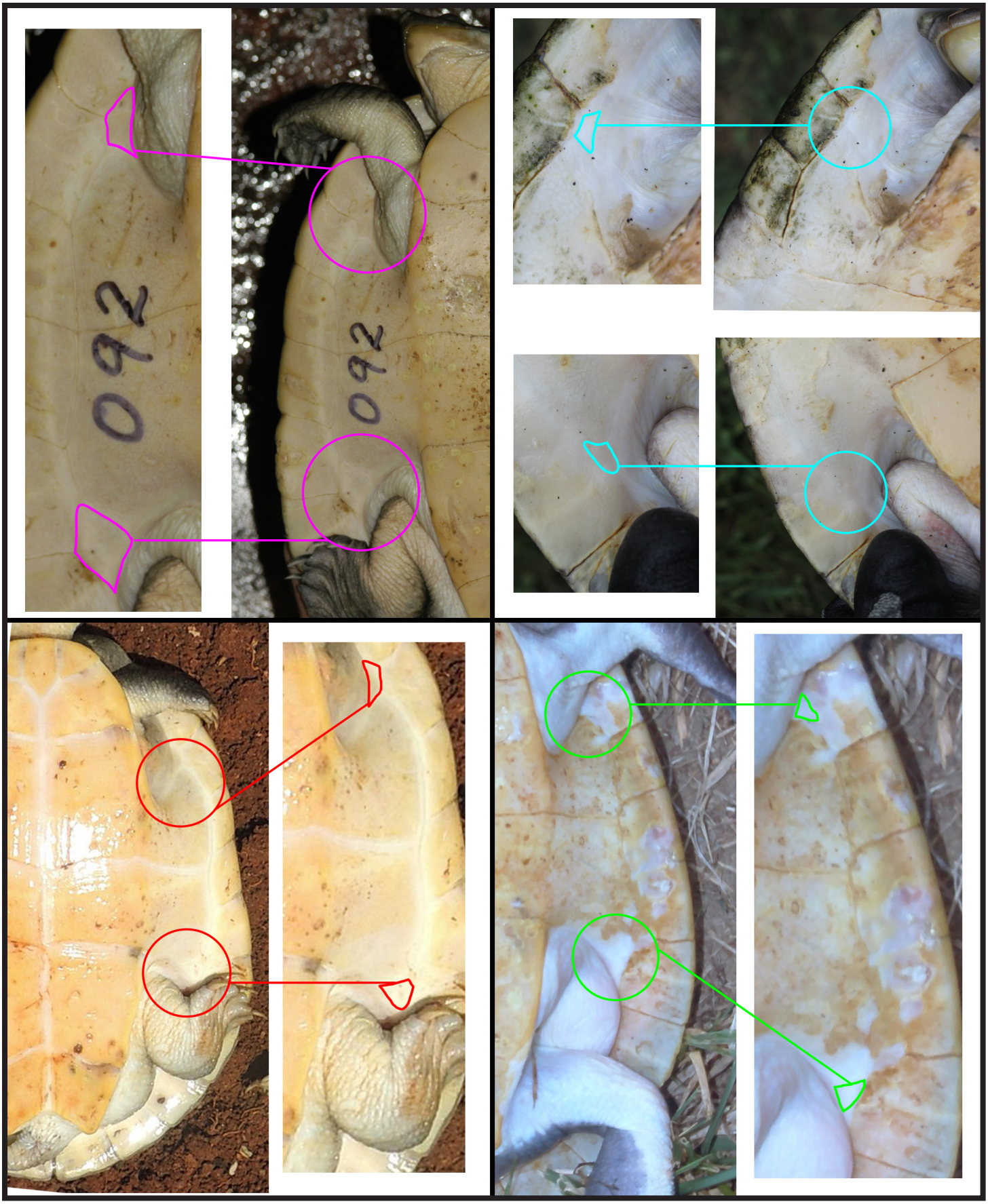

Figure 13. Axillary and inguinal scutation in *Elseya (Hanwarachelys)*, continued: *E. caelatus caelatus* (top left - Inawantan); *E. caelatus ayamaru* (top right- Ayamaru); *E. orestiad* (bottom left - Dair Bay); *E. rhodini* (bottom right - Balimo), all live.

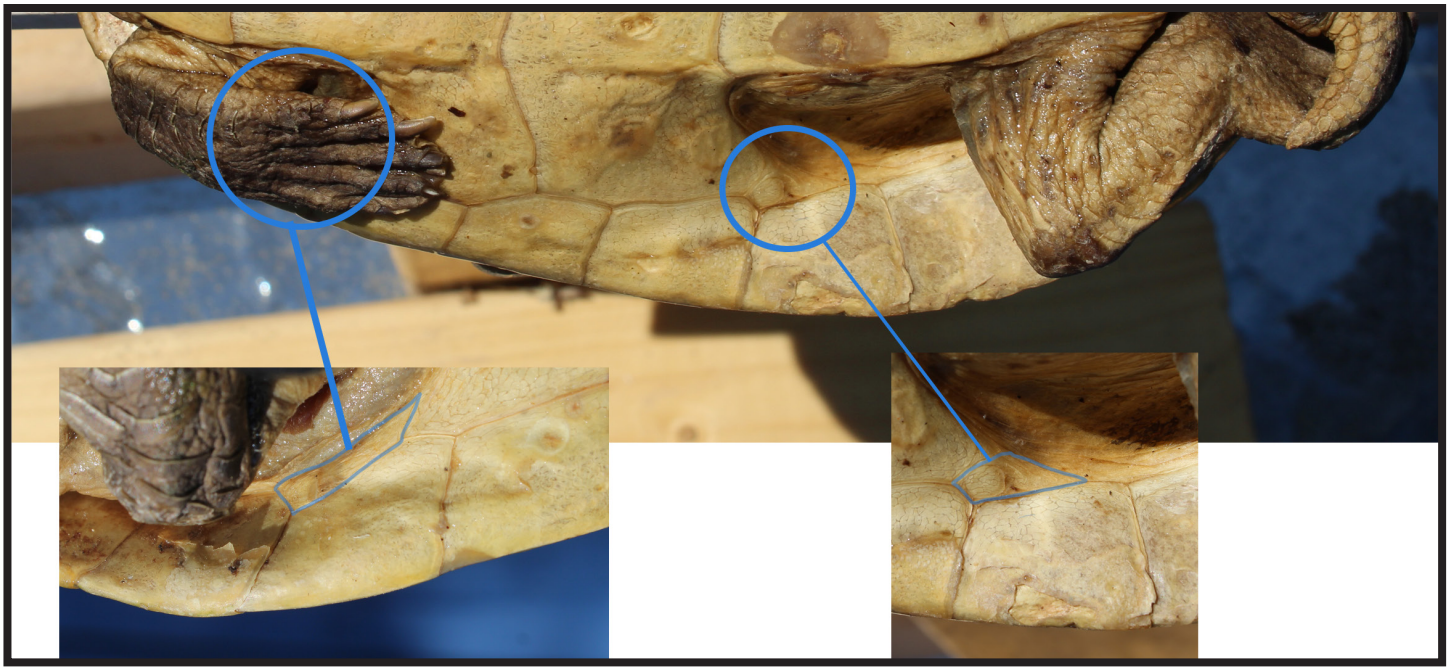

Figure 14. Inframarginal condition in the male holotype of *Elseya (Hanwarachelys) calaetus berau,* a recently described subspecies that was considered potentially extinct but has been found extant (Joseph-Ouni & McCord, i*n prep.*).

The *Elseya* subgenus *Hanwarachelys* possesses both scutes, well-defined, and showed the most variation from species to species.

In *E. (H.) novaeguineae* (n = 8), the axillary is a relatively small-sized triangle with one side in full contact with the posterior-most portion of marginal 3 and extending to the anterior-most portion of marginal 4 (Figure 12). The inguinal is a large polygon with the longest side bordering the hypoplastral skin, the opposing side sharing a sulcus with posterior marginal 7 and one side extending from anterior to middle marginal 8. In two specimens both scutes were absent.

In *E. (H.) schultzei* (n = 8), the axillary scute was a consistently large polygon, with the shortest side sharing a sulcus with the posterior of marginal 3, one long side sharing a sulcus with marginal 4 to its anterior-middle to posterior-middle (Figure 12). The inguinal scute had a few variations (small to large triangle; small polygons) but typically was a strongly defined (strongly delineated sulcus) polygon similar to *E. (H.) novaeguineae)* but larger, such that its shortest side was in full contact with the entire posterior third of marginal 7 with one long side sharing the sulcus with the anterior half of marginal 8.

In *E. (H.) caelatus caelatus* (n = 3, Figure 13), the axillary scute is small-sized and, polygonal, with one side sharing the posterior third of marginal 3 sulcus and the next side sharing the anterior third of marginal 4 sulcus. The inguinal is relatively large, a diamond-shaped polygon, with one side sharing the posterior half (or third) of marginal 7 sulcus and the next side sharing the anterior half (or third) of marginal 8 sulcus.

In *E. (H.) caelatus ayamaru* (n = 3, Figure 13), the axillary scute is much smaller than the nominate form, polygonal, with one side sharing the posterior-most portion of marginal 3 sulcus and the next side sharing the anterior quarter of marginal 4 sulcus. The inguinal is also smaller, being a rounded triangle with one side sharing the anterior half (or third) of marginal 8 sulcus.

In *E. (H.) caelatus berau* (n = 2, Figure 14), the axillary scute is a large, elongated polygon with one side sharing the posterior-most portion of the marginal 3 sulcus and the next side sharing the anterior three-quarters of the marginal 4 sulcus. The inguinal is smaller, being a trapezoidal shape with one side sharing the posterior-most portion of marginal 7 sulcus and anterior two-thirds of marginal 8 sulcus.

In *E. (H.) orestiad* (n = 3, Figure 13), the axillary scute is a small polygon with one side sharing the posterior-most portion of marginal 3 sulcus and the next side sharing the anterior third of marginal 4 sulcus. The inguinal is also

small, being polygonal, with the shortest side sharing the posterior-most portion of marginal 7 sulcus, and a long side sharing the anterior half of marginal 8 sulcus.

In *E. (H.) rhodini* (n = 3, Figure 13), the axillary scute is a small equilateral triangle with one side sharing the anterior-third to half of marginal 4 sulcus. The inguinal is also a small triangle, with the hypotenuse sharing the anterior half of marginal 8 sulcus.

In *E. (H.) timika timika* (n=3, Figure 15) the axillary scute is a large elongated polygon with a common sulcus from posterior most M3 to middle M4. The inguinal scute is a small asymmetrical triangle with common sulcus typically at middle M8.

In *E. (H.) timika aru* (n=3, Figure 15) the axillary scute is a small elongated polygon with a common sulcus from posterior most M3 to middle M4. The inguinal scute is a small asymmetrical polygon with common sulcus from posterior most M7 to middle M8.

In *E. (H.) timika paniai* (n=2, Figure 16) the axillary scute is a small elongated polygon with a common sulcus from posterior most M3 to anterior M4. The inguinal scute is a large asymmetrical polygon with common sulcus at posterior-middle M7 to anterior-middle M8.

In *E. (H.) timika wamena* (n=2, Figure 16) the axillary scute is a smalll elongated polygon with a common sulcus from posterior most M3 to anterior M4. The inguinal scute is a small asymmetrical polygon with common sulcus at posterior M7 to middle M8.

In *E. (H.) freweri* (n=2, Figure 17) the axillary scute is a symmetrical elongated polygon with a common sulcus from posterior most M3 to middle M4. The inguinal scute is a mid-sized asymmetrical triangle or polygon with common sulcus typically at posterior M7 to anterior M8.

In *E. (H.) papua* (n= 5, Figure 18), the axillary scute is a small unequal polygon with one side sharing the anterior-third to half of the marginal 4 sulcus. The inguinal is relatively large with one short side sharing the posterior one-fourth of marginal 7 sulcus and one long side sharing the anterior half to two-thirds of the marginal 8 sulcus.

In *E. (H.) nabire* (n= 5, Figure 18), the axillary scute is consistently absent in the spcimens examined and the inguinal is a reduced small triangle, with one side sharing the middle portion of the marginal 8 sulcus.

In the *Elseya* subgenus *Solomonemys* (n = 1 per species, Figure 18), the axillary and inguinal scutes are present in both specimens of the two known species, with the inguinal scutes being larger than the axillaries.

The axillary scute in *E. (S.) eidolon* is small, and approximates a trapezoidal polygon, with one side sharing a sulcus with the posterior third of M3 and one side sharing the anterior third M4 sulcus. The inguinal scute is large, approximating a diamond, with one side sharing the posterior third of the M7 sulcus and one side sharing the anterior half of M8 sulcus.

The axillary scute in *E. (S.) auramemoria* is small, and approximates a polygon, with one side sharing a sulcus with the posterior third of M3 and one side sharing the anterior half of M4 sulcus. The inguinal scute is relatively large, approximating a polygon with one side sharing the posterior-most portion of the M7 sulcus and one side sharing the anterior half of M8 sulcus.

CONCLUSION & SUMMARY

While the presence of full inframarginals has been a feature of many extinct basal families of turtles and thereafter through chelonian evolution, mostly confined to the cryptodiran lineages, and in fossil species of extant families, they are found today in only a few families, in the cryptodires.

Without a full series of inframarginals, other families possess axillary and inguinal scutes. While only two of the three extant families of Pleurodira have at least some species that retain these scutes in part, they are relatively insignificant in size, often only one of them is present. They are so reduced that they are typically overlooked entirely, possibly since their positions on the bridges are normally associated with the Rathke's glands. Indeed, for the majority of living Pleurodires, the thin laminae surrounding and/or accommodating the external pores of the glands are the only associated portion of the bridge present (where axillary and inguinal scutation would occur).

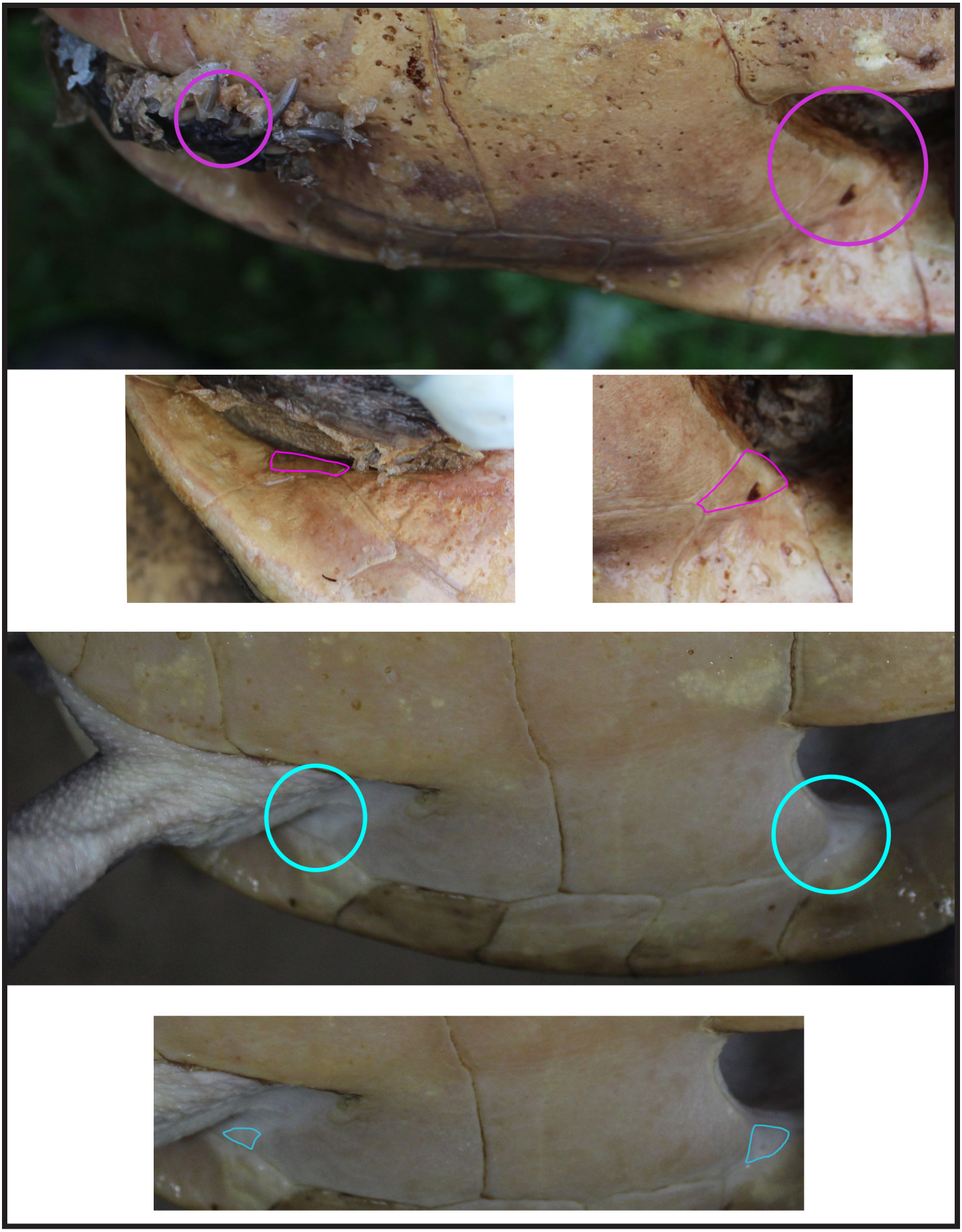

Figure 15. Axillary and inguinal scutation in *Elseya (Hanwarachelys)*, continued: *E. timika timika* (top, female, preserved type); *E. timika aru* (bottom, female, live specimen).

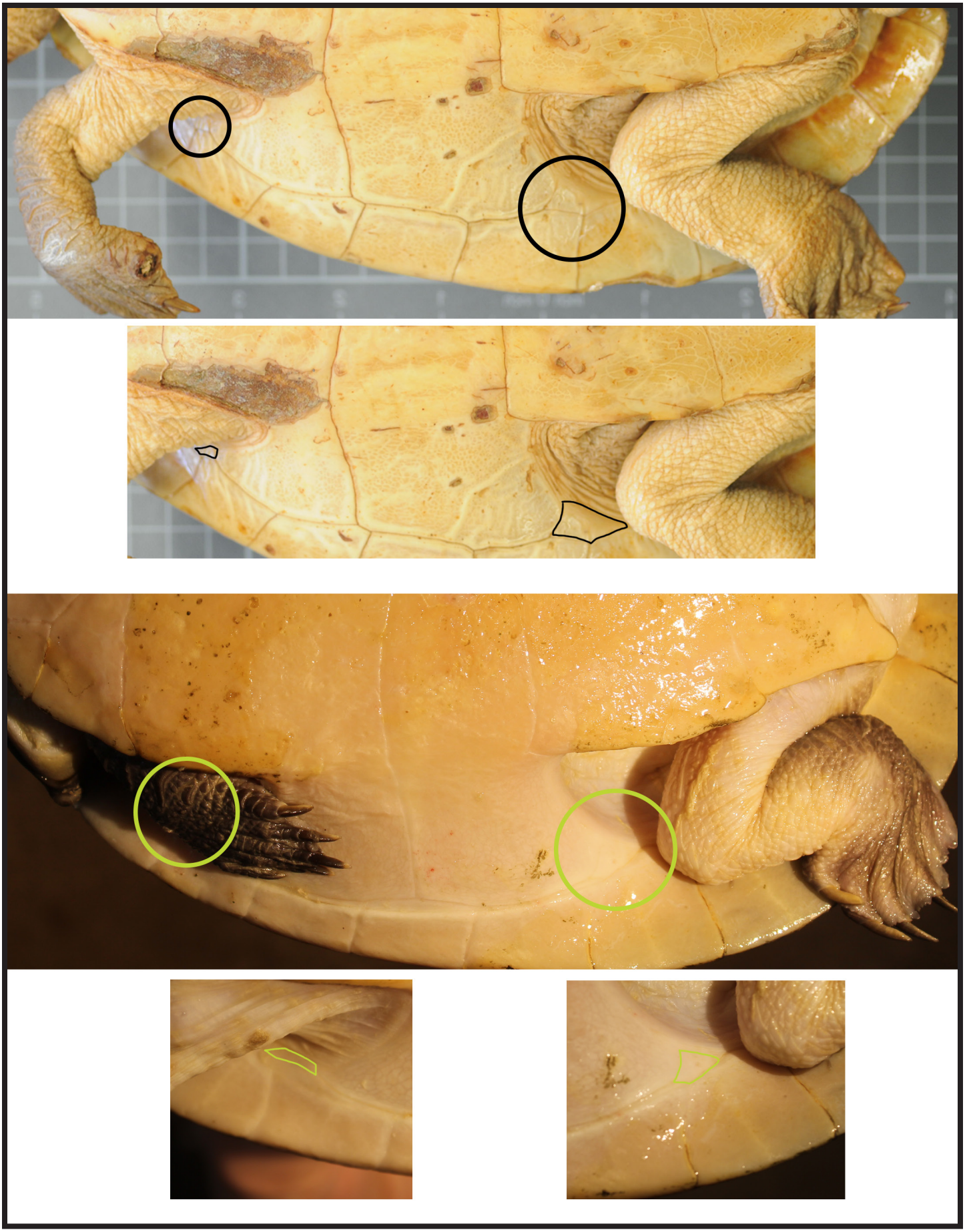

Figure 16. Axillary and inguinal scutation in *Elseya (Hanwarachelys)*, continued: *E. timika paniai* (top, female holotype); *E. timika wamena* (bottom, female); both live.

Figure 17. Axillary and inguinal scutation in *Elseya (Hanwarachelys)*, continued: *E. freweri* (top, female holotype, in life).

In Australasian chelid turtles, axillary and inguinal scutes occur in only a few short-necked genera. The long-necked species unequivocally lack them, as do a few short-neck genera. Some short-necked genera including *Emydura* and *Elseya ('Pelocomastes')* contain species that bear either axillary or inguinal scutes or both, but only as variants in a few specimens (potentially vestigial of the condition in which they were consistently present). Among these, we found no species in which scutation was consistent.

Elusor, Rheodytes and two subgenera of *Elseya* (*Elseya* and *Hanwarachelys*) almost always possess both axillary and inguinal scutes which, while showing what may be normal variation in shape and size, were consistent in species to species amongst the specimens examined.

The scutes in *Elusor* and *Rheodytes* are well-defined in shape and size and we suggest that the descriptions of them presented in the discussion and plates can be incorporated in future diagnoses of those taxa. The same can be said of *Elseya dentata* (which showed the largest axillary and inguinal scutes of all Australasian chelids) and *E. jukesi/ flaviventralis* (relatively large in size but consistent in shape and position).

One surprising find is that the condition of these scutes in those two Northern Territory species differed substantially from *E. branderhorsti*, their close relative from New Guinea. In the latter species several specimens lacked axillary scutes, while others possessed relatively small ones and still others, large ones. The inguinal scute was present, similarly shaped in various specimens but surprisingly reduced in size with lack of well-defined sulcus borders. These observations should be tested on additional specimens from other populations, as only the Merauke population and some photographs of the Bensbach River population were available. Notably, in the single known recent specimen of the extant *E. lavarackorum*, the inguinal scute is markedly similar to most *E. branderhorsti*; these two taxa were considered closest relatives by Joseph Ouni *et al.* (2023).

The species of *Elseya* subgenus *Hanwarachelys* showed more consistency in shape than in size within each species,

Figure 18. Axillary and inguinal scutation in *Elseya (Hannarachelys)*, continued: *E. papua* (top left - Muting, Indonesia); *E. nabire* (top right- Nabire, Indonesia); and in *Elseya (Solomonemys)* : *E. eidolon* (bottom left - holotype, Malaita, Solomon Islands); *E. auramemoria* (bottom right - holotype, Guadalcanal, Solomon Islands), all in life.

although the size and positioning of each varied to the extent that we consider a normal part of individual variation. Shapes fell into two broad categories: polygonal in *E. novaeguineae, E. caelatus* (all ssp.), *E. papua, E. schultzei*, *E. orestiad, E. timika* (all ssp.), *E. freweri* and triangular in *E. rhodini* and *E. nabire*. *E. nabire* consistently lacked axillary scutes, and the inguinal scutes are small. For the polygonal group, we suggest that these scutes are present consistently in shape, relative size and positioning to a degree that could be diagnostic for these taxa.

For *E. rhodini* sensu stricto, additional populations should be tested, as only photographs of specimens from Balimo and Kikori were available. Other populations that were assigned to that taxon, especially from the Timika regions to Merauke, Papua Province, Indonesia were featured in a revision of this complex by Joseph-Ouni & McCord (2023).

As the two *Elseya (Solomonemys)* species are known currently by one specimen each, it is not possible to measure consistency of the scutes, however the scutes are present in both known specimens and well-defined.

Of all species documented here to possess the scutes, or to possess them as occasional variants, we did not detect any trend that could be attributed to sexual dimorphism. Nor do we consider any patterns attributable to ontogeny, as we carefully selected only fully adult specimens.

In summary, neither axillary nor inguinal scutes were documented in any taxa of *Chelodina* (all three subgenera) with the exception of a single instance in a specimen of *C. novaeguineae* but which we consider an abnormality. In *Emydura*, the axillary scute was normally entirely absent, but sometimes present in specimens although inconsistently (i.e. no species specific correlation) and hence considered as a variant or vestigial, while the inguinal was almost always simply a thin lamina around the external pore of Rathke's gland and not qualifiable. In *Pseudemydura* these scutes were absent. In *Wollumbinia* the axillary scute was absent and the inguinal area was so reduced to not be considered further (hence absent). In the *Elseya* subgenus *'Pelocomastes'*, axillary and inguinal scutes were extremely reduced when occurring, but like *Emydura* occurred so sporadically as to not be reliable. They were entirely absent in most cases and were not considered further because they were inconsistently present within species (hence considered only a specimen variant).

In *Rheodytes, Elusor* and the *Elseya* subgenera *Elseya* and *Hanwarachelys*, axillary and inguinal scutes were consistently present, relatively large in size and well-defined by sulci. *Elseya dentata* normally possessed the largest scutes, while *Elseya branderhorsti* showed the most variation in size in the axillary scute, being absent, small or large across specimens and the inguinal scutes relatively small. In the new described subgenus *Solomonemys* of the genus *Elseya* axillary and inguinal scutes were present and strongly demarcated; however the comprised taxa are only known from the holotypes (Joseph-Ouni *et al.* 2022).

ACKNOWLEDGMENTS & PHOTOGRAPHY CREDITS

The authors offer their appreciation and gratitude as follows:

Patrick Couper, Andrew Amey and the Queensland Museum and support staff, Australia; Australian Museum for access (RAS) to collections; Nick Hostetter for assistance with photography of New Guinea *Elseya*; Glenn Shea for personal communications ~2020; Gavin Dally of MAGNT for specimen images; Gregory Watkins-Colwell, Division of Vertebrate Zoology, Yale Peabody Museum; Stevie Kennedy-Gold and Joseph Martinez (Herpetology Department, Harvard Museum of Comparative Zoology); David Kizirian, Lauren Vonnahme and David Dickey, Herpetology, Vertebrate Zoology, American Museum of Natural History); Ian Smales for guidance on the original manuscript; Paul Vander Schouw and an anonymous reviewer for corrections and helpful recommendations for improvement.

Photography credit is due as follows: Title Page, Figure 19: J. Cann; Figure 1: J. Frewer; Figure 2: J. Cann except *C. novaeguineae* W.P. McCord
Figure 3: W.P. McCord except *E. australis* R. Sadlier
Figure 4: *E. albagula* (Holotype),© 2020, Queensland Museum, Peter Waddington; *W. purvisi* J. Cann; Figure 5: G. Dally
Figure 6: *E. macrurus* (Holotype), © 2020, Queensland Museum, Peter Waddington; J. Cann
Figure 7: J. Cann; *R. leukops;* (Holotype), © 2004, Queensland Museum, Vince Railton.
Figure 8: J. Cann (top); J. Frewer (bottom left); R. Sadlier (bottom right); Figure 9: *E. jukesi*/ *flaviventralis* R. Sadlier; *E. branderhorsti* W.P. McCord
Figure 10: *E. kalumburu* R. Sadlier; *E. sahul* G. Dally; Figure 11: *E. lavarackorum* Les McKenzie; Figure 12: W.P.McCord & A. Georges
Figure 13: W.P. McCord; *E.c. caelatus* W.P.McCord & A. Georges; All other figures, senior author.

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Figure 19. Habitat of *Elseya dentata* along the Victoria River, Northern Territory, Australia.

APPENDIX

Summary of axillary and inguinal scutes occurrence or absence in Australasian chelid taxa.
x = not present; ~ = typically absent but with individual variant; * = present but extremely variable; ✓= present.

Scute	Axillary	Inguinal	Number Examined
Species			
All Chelodina	x	x	3 per species[1]
Pseudemydura	x	x	3
All Emydura	~	~	3 per sp/ssp
All Wollumbinia	~	~	3 per species
Elusor	✓	✓	4
Rheodytes	✓	✓	4
Elseya			
All (Pelocomastes)	~	~	3 per species
(Elseya)			
dentata	✓	✓	10
jukesi/flaviventralis	✓	✓	4
branderhorsti	*	✓	8
sahul	✓	✓	3
kalumburu	✓	✓	3
lavarackorum	✓	✓	1
(Hanwarachelys)			
novaeguineae	✓	✓	8
schultzei	✓	✓	8
rhodini	✓	✓	3
orestiad	✓	✓	3
papua	✓	✓	5
nabire	x	✓	5
caelatus caelatus	✓	✓	3
caelatus ayamaru	✓	✓	3
caelatus berau	✓	✓	2
timika timika	✓	✓	3
timika aru	✓	✓	3
timika paniai	✓	✓	2
timika wamena	✓	✓	2
freweri	✓	✓	2
(Solomonemys)			
auramemoria	✓	✓	1
eidolon	✓	✓	1

1.Except *C. kuchlingi*, 1 specimen