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Systematic revision of the genus *Everettia* Godwin-Austen, 1891 (Mollusca: Gastropoda: Dyakiidae) in Sabah, northern Borneo

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The species of the snail genus *Everettia* in the Malaysian state of Sabah are superficially similar and difficult to distinguish by their shells. This paper presents new data on the taxonomy and distribution of *Everettia* in Sabah that have accumulated since the revision by Godwin-Austen in 1891. By using morphological and molecular phylogenetic approaches, we reveal at least seventeen species of *Everettia* in Sabah, of which eleven are new to science, namely: ***Everettia layanglayang* sp. nov.**, ***Everettia lapidini* sp. nov.**, ***Everettia paulbasintali* sp. nov.**, ***Everettia occidentalis* sp. nov.**, ***Everettia jasilini* sp. nov.**, ***Everettia safriei* sp. nov.**, ***Everettia interior* sp. nov.**, ***Everettia jucundior* sp. nov.**, ***Everettia planispira* sp. nov.**, ***Everettia monticola* sp. nov.**, and ***Everettia dominiki* sp. nov.**, and one new subspecies, namely, ***Everettia corrugata williamsi* ssp. nov.** Phylogenetic analysis of mitochondrial *COI* and *16S*, and nuclear *ITS-1* sequences demonstrates the monophyly of most of the morphologically well-defined species. Our results show that certain aspects of classical morphology-based taxonomy for *Everettia* species, especially with regard to the unique combination of shell surface sculptures, animal head colour, and mantle pigmentation, are solid. A dichotomous key to the Sabah species and subspecies of *Everettia* is provided.

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ADDITIONAL KEYWORDS: biogeography – coloration – land snails – Malaysia – mantle pigmentation – molecular phylogeny – Mount Kinabalu – shell sculpture – South-east Asia.

INTRODUCTION

South-east Asia is recognized as one of the biodiversity hotspots of the world (Myers *et al*., 2000). Several thousands of land snail species are known from this area so far (Benthem Jutting 1948, 1950, 1952; Solem, 1966; Maassen, 1997, 2001; Muratov & Abdou, 2006 and references therein). Several recent studies in South-east Asian caenogastropod land snails have demonstrated that many previously overlooked new species could be detected by intensive taxonomic revision (Vermeulen, 1991, 1994). However, the taxonomy of many of the Pulmonata land snail genera remains unreliable.

Everettia is the most species-rich genus in the family Dyakiidae in Borneo, despite its simplified helicoid shell (Hausdorf, 1995; Schileyko, 2003). Until the 1930s, at least 16 *Everettia* species were described, mainly from west and north-west Borneo. Since then, however, a critical revision of the taxonomy has not been attempted and the genus remained to be viewed as a notoriously difficult group to work with. As Smith (1895) wrote, 'nearly all the species in this genus (*Everettia*) are exceedingly difficult to distinguish by their shell, and it is quite

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impossible to determine them from the published description or even the figures.' Solem (1964) said that 'the shell of the fifteen species of *Everettia* are very similar in color and form, usually also in size.' As a result of the paucity of diagnostic characters, the descriptions of the species were mostly short and imprecise. Moreover, a considerable degree of geographical variation could be discerned in shell morphology. For instance, Godwin-Austen (1891) found that shell morphology is localized – shells at each location were similar to each other but differed from the shells from other places when he was arranging a series of collections in the British Museum. As a result, he conservatively suggested that many of those might be local varieties of earlier described species.

Despite shell morphology initially offering little prospect of resolving the taxonomy, anatomical data were scarce from the start. In almost no 19th century species descriptions were details of the anatomy included, but anatomical data were included in a subsequently described species (i.e. *Everettia corrugata sensu* Laidlaw, 1937) and added to a few of the previous described species [e.g. *Everettia jucunda sensu* Pfeiffer (1863) by Godwin-Austen (1891) and *Everettia subconsul* (?) *sensu* Smith (1887b) by Laidlaw (1931)]. In addition to the lack of detailed conchological data, many of these species were described on the basis of only a few specimens and unspecified type localities have further restrained the efforts of improving knowledge of this genus.

Previous studies (e.g. Smith, 1895) had shown that classification based on morphological data was very unsatisfactory in *Everettia*. In many similar complex snail genera, genetic data and microscopic characters have proven useful in solving the taxonomic puzzle (Uit De Weerd & Gittenberger, 2004; Zelaya, Absalão & Pimenta, 2006) and a similar approach may also prove useful in *Everettia*. This would be particularly timely, because many samples of *Everettia* have been collected in Sabah since the establishment of the BORNEENSIS mollusc collection at Universiti Malaysia Sabah (BOR/MOL) and the mollusc collection in the Sabah Parks Museum (SP). In view of the scattered literature and lack of a summary of the *Everettia* species in Sabah, it was thought worthwhile to review the taxonomy, phylogeny, and distribution of this genus. Thus, in addition to the shell and soft part morphology, we also obtained genetic data from nuclear and mitochondrial loci. In this paper, we (1) revise the taxonomy of *Everettia* spp. in Sabah, northern Borneo; (2) explore the phylogenetic relationships among *Everettia* species; and (3) investigate the usefulness of genetic, shell morphology, animal pigmentation, and genital anatomy data in resolving the classification. We limit our scope to Sabah *Everettia* species after considering the fact that after checking the material in Jaap Jan Vermeulen's private collection, Leiden (JJ), the National the Museum of Natural History, Leiden 'Naturalis' (RMNH), the Zoological Museum of Amsterdam (ZMA), and the Natural History Museum, London (BMNH), non-Sabah material is insufficient for a Borneo-wide revision, especially in view of the fact that many species are short-range endemics.

MATERIAL AND METHODS

MORPHOLOGY

Four-hundred and fifty-one lots of ethanol-preserved and dry *Everettia* specimens were examined. Shell dimensions were measured with vernier callipers to the nearest 0.1 mm. Shell height is the maximum dimension parallel to the axis of coiling, shell width the maximum dimension perpendicular to shell height. As the adult of *Everettia* does not have an apertural lip, it is usually not possible to determine whether a shell is adult. Thus, only the maximum shell height and width are given in the description, rather than the range of the adult size. We also measured aperture height and width, and the respective widths for the first, second, and third whorls. Counting of the shell whorls follows Hoenselaar & Goud (1998) and Vermeulen & Whitten (1998). Details of shell surface and underside microsculpture were visible at low magnification (30×) but photographs were taken with a scanning electron microscope after coating of specimens with platinum. This microsculpture above the periphery was classified into four categories, namely, (1) granular sculpture; (2) prominent radial riblets; (3) spiral grooves; and (4) essentially smooth.

As we have limited wet material (Table 1), we do not quantify the anatomical differences amongst species, but for some species notes on representative genital characters are provided. These comprise maximum length from the genital opening to the end of the dart-sac (before the visible gland tubules); and qualitative descriptions for the arrangement of the penis (P), vagina (V), genital opening (GO), bursa copulatrix (BC), and dart-sac (DS) around the genital atrium. The length ratio of BC and DS is also given. There are two main groups of animal head colour patterns: (1) uniform in colour; and (2) with a white band between the eye-tentacles. Mantle pigmentations are also grouped into categories, namely, (1) sparse irregular black and bright marking; (2) regularly radially spaced darker brown bands; and (3) brighter spots arranged regularly. We constructed the dichotomous key by using both shell and animal morphological characters.

Table 1. Species list indicating the number of dissected specimens, locality, and GenBank accession numbers

No.	Species	Dissected specimens	Morphology			Locality	16S	COI	ITS
			Shell*	Mantle†	Head‡				
1	*Everettia jucunda*	0	**3**	**2**	**2**	Beaufort, Klias	FJ160635	FJ160682	FJ160723
2						P. Tiga	FJ160636	FJ160683	FJ160724
3	*Everettia subconsul*	12	4	2	2	Mt Tambuyukon eastern slope, 1100 m S114	FJ160629	FJ160676	FJ160719
4						Crocker Range, Ulu Membakut	FJ160630	FJ160677	FJ160720
5						Crocker Range, Ulu Membakut	FJ160631	FJ160678	FJ160721
6						Crocker Range, Kimanis 14–16 km, SP12529	FJ160632	FJ160679	–
7						Crocker Range, Kimanis 14–16 km, SP12529	FJ160633	FJ160680	–
8						Danum Valley CC	FJ160639	FJ160686	FJ160727
9						Nalapak Substesen Kinabalu	FJ160640	FJ160687	FJ160728
10						Nalapak Substesen Kinabalu	FJ160641	FJ160688	–
11						Kota Kinabalu, Pulau Gaya	FJ160634	FJ160681	FJ160722
12	*Everettia themis*	2	4	2	1	Crocker Range TBC tower sp12599	FJ160623	FJ160670	FJ160713
13						Mt Kinabalu southern slope, *c.* 1500 m	FJ160627	FJ160674	FJ160717
14						Mt Kinabalu southern slope, *c.* 1900 m	FJ160628	FJ160675	FJ160718
15	*Everettia klemmatanica*	2	1	2	2	Mt Kinabalu southern slope, *c.* 1700 m	FJ160611	FJ160660	FJ160704
16	*Everettia corrugata corrugata*	11	4	1	1	Mt Kinabalu north-western slope, 3000 m S142	FJ160619	FJ160666	FJ160710
17						Mt Kinabalu southern slope, 3100 m S14	FJ160620	FJ160667	–
18						Mt Kinabalu southern slope, 3400 m S16	FJ160621	FJ160668	FJ160711
19	*Everettia corrugata williamsi*	4	1	1	1	Mt Kinabalu south-eastern slope, 3100 m S69A	FJ160622	FJ160669	FJ160712
20	*Everettia layanglayang*		4	3	1	Mt Kinabalu north-western slope, S132	FJ160624	FJ160671	FJ160714
21						Mt Kinabalu south-eastern slope, S58	FJ160625	FJ160672	FJ160715
22						Mt Kinabalu southern slope, S11	FJ160626	FJ160673	FJ160716
23						Crocker Range, Gunung Alab (1800 m)	FJ160643	FJ160690	–
24						Crocker Range, Gunung Alab (1800 m) SP12907	FJ160644	FJ160691	FJ160730
25	*Everettia lapidini*	2	3	2	1	Mt Kinabalu south-western slope, *c.* 1700 m, Marai Parai SP12924	FJ160645	FJ160692	FJ160731
26	*Everettia interior*	3	**3**	**2**	**2**	Sapulut, Batu Tinagas	FJ160637	FJ160684	FJ160725
27						Sapulut, Batu Sanaron	FJ160638	FJ160685	FJ160726
28	*Everettia paulbasintali*		2	2	2	Tawau Hills Park (HQ)	FJ160613	FJ160662	FJ160706

Table 1. *Continued*

No.	Species	Dissected specimens	Morphology			Locality	16S	COI	ITS
			Shell*	Mantle†	Head‡				
29						Tabin Wildlife Reserve (HQ)	FJ160642	FJ160689	FJ160729
30	*Everettia jucundior*	2	**3**	**2**	**2**	Tawau Hills Park (HQ)	FJ160612	FJ160661	FJ160705
31	*Everettia jasilini*	2	1	1	1	Mt Kinabalu north-eastern slope, 3100 m S80	FJ160617	FJ160664	FJ160708
32						Mt Kinabalu north-western slope, 2800 m S140	FJ160618	FJ160665	FJ160709
33	*Everettia safriei*	8	4	1	1	Mt Kinabalu north-eastern slope, 3300 m S79	FJ160614	FJ160663	FJ160707
34						Mt Kinabalu north-eastern slope, 3300 m S82	FJ160615	–	–
35						Mt Kinabalu southern slope, 2400 m S47	FJ160616	–	–
36	*Everettia planispira*	0	4	1	2	Tawau Hills Park (HQ)	FJ160595	FJ160647	FJ160694
37						Mt Tambuyukon north-eastern slope, 1700 m S126	FJ160609	–	FJ160703
38	*Everettia monticola*	3	4	1	2	Mt Kinabalu southern slope, 1700 m S32	FJ160596	FJ160648	FJ160695
39	*Everettia dominiki*	8	2	1	2	Mt Kinabalu southern slope, 2100 m S30	FJ160597	–	–
40						Mt Kinabalu south-western slope, 2100 m S100	FJ160598	FJ160649	FJ160696
41						Mt Tambuyukon eastern slope 2200 m S102	FJ160599	FJ160650	FJ160697
42						Mt Kinabalu north-western slope, 2500 m S135	FJ160600	FJ160651	–
43						Mt Kinabalu south-western slope, 2600 m S96	FJ160601	FJ160652	–
44						Mt Kinabalu south-western slope, 2600 m S97	FJ160602	FJ160653	–
45						Mt Kinabalu southern slope, 2600 m S50	FJ160603	FJ160654	–
46						Mt Kinabalu north-western slope, 2600 m S138	FJ160604	FJ160655	FJ160698
47						Mt Kinabalu south-western slope, 2900 m S90	FJ160605	FJ160656	FJ160699
48						Mt Kinabalu south-eastern slope, 3100 m S68	FJ160606	FJ160657	FJ160700
49						Mt Kinabalu south-western slope, 3100 m S87	FJ160607	FJ160658	FJ160701
50						Mt Tambuyukon eastern slope, 1100 m S113	FJ160608	FJ160659	FJ160702
51						Mt Tambuyukon eastern slope, 2000 m S107	FJ160610	–	–
52	*Quantula striata*	1	–	–	–	Singapore	FJ160646	FJ160693	FJ160732
							52	47	39

*Shell surface sculpture: (1) granular sculpture; (2) prominent radial riblets; (3) spiral grooves; and (4) almost smooth.
†Mantle pigmentation: (1) sparse irregular black and bright markings; (2) radial regularly spaced dark brown bands; and (3) bright spots arranged regularly.
‡Animal head colour: (1) uniform in colour; and (2) white band in between eye tentacles.
Bold text indicates that all three morphological characters are the same for these three species. Underlined text indicates that all three morphological characters are the same for these two species.

Molecular genetics

We sequenced DNA from a total of 51 individuals, which helped to recognize 16 species and subspecies (Table 1; Supporting Information Appendix S1). At least one individual for each of the species described in this paper, except *Everettia occidentalis*, was sequenced. We also included an outgroup taxon – *Quantula striata* Gray, 1834 (Dyakiidae). All the samples for molecular genetic analysis were collected between 2004 and 2008.

Genomic DNA from approximately 2–3 mm^3 of foot tissue of single individuals was extracted using DNeasy nucleic acid extraction kits (QIAGEN) or a phenol–chloroform protocol (Tachi, Takano & Schilthuizen, 2003). DNA was eluted in autoclaved Tris-ethylenediaminetetraacetic acid buffer and stored at –20 °C. PCR was performed using a PTC-200 thermocycler (MJ Research, Inc.) to amplify the mitochondrial DNA region of *16S* with the primer pair 16Sbr-L and 16Sbr-H (Palumbi *et al*., 1991), and *COI* with primers LCO1490 and HCO2198 (Folmer *et al*., 1994). We also amplified the nuclear rDNA region of *ITS-1* with the primer pair 5.8c 'silkworm' and 18d 'fruitfly' (Hillis & Dixon, 1991). Reactions were performed in 50-μL volumes, using 5 μL 10 × reaction buffer (Promega), 5 μL 2 mM deoxyribonucleotides (dNTP), 6 μL 25 mM $MgCl_2$, 2 μL for each primer (5 pmol), 26.85 μL de-ionized autoclaved water and 1 unit of Taq polymerase (Promega). The following cycling profile was used: 2 min at 95 °C, followed by 35 cycles of 1 min at 95 °C, 1 min at 55 °C for *16S* and *COI* (60 °C for *ITS-1*) and 2 min at 72 °C, and a final extension period of 10 min at 72 °C.

Ten-μL PCR products were taken and checked via agarose gel (1%) electrophoresis. PCR-amplified DNA fragments were purified with the Roche Purification Kit, according to the manufacturer's protocol. Then, DNA sequencing was performed directly on purified PCR products for both directions by using the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems Ltd), and visualization of results was carried out on an ABI 3100 Genetic Analyser (Applied Biosystems Ltd).

Sequence analysis

Electropherograms were checked by eye and, if reading errors had been made by Genetic Analyser, corrected. The DNA sequences were aligned using the ClustalW Multiple alignment algorithm in the BioEdit Sequence Alignment Editor, version 7.0 (Hall, 1999), then subsequently checked and adjusted manually using the same program. Absolute pairwise percentage sequence divergences (genetic *p*-distances) between species and within species were calculated using MEGA 4 (Tamura *et al*., 2007).

Phylogenetic relationships were analysed using maximum parsimony (MP), with PAUP*4.0b10 (Swofford, 2002) and Bayesian analysis (BA) with MrBayes 3.1 (Huelsenbeck & Ronquist, 2001). The analyses were run for the combined dataset of *ITS-1*, *COI*, and *16S* genes, and for each gene separately. We also repeated the analyses for the respective gene after excluding the region that could not be aligned unambiguously (*16S* and *ITS-1*) and the third codon position of *COI*. For MP, gaps were included as a fifth character state and each character was given equal weight. Five hundred bootstrap replicates were carried out, with ten replicates of a heuristic search with random addition sequence at each bootstrap replicate. Branches were swapped under the tree bisection reconnection (TBR) algorithm. MODELTEST 3.7 (Posada & Crandall, 1998) was used to find the best substitution model from 56 models for all seven data matrices (Supporting Information Appendix S2). Based on these selected substitution models, each respective data matrix was analysed in BA with 1 000 000 generations and sampled every 100th generation. We then discarded 25% of the samples obtained during the first 1 000 000 generations. BA was repeated three times for each data matrix and a consensus tree with a cut-off value of 50 % was calculated for the resultant trees.

RESULTS 1: SYSTEMATIC PART

At least 16 *Everettia* species were previously described from Borneo (Supporting Information Appendix S3). However, the animal and anatomy of these previously described species were unknown. Therefore, it is possible that many of these so-called *Everettia* spp. might not belong to the genus. Conversely, the anatomy of many species in other genera was also poorly known. Thus, it is also possible that some of the species in other genera also belong to *Everettia* after examination of the anatomy. We limited our scope to only the shells/snails that were found in Sabah for the reasons given above. *Everettia* appears to be restricted to Borneo (Kobelt, 1870; Gude, 1902; Laidlaw, 1932; Solem, 1966; Hausdorf, 1995).

In addition to the *Everettia* material listed in this paper, we evaluated all material in the BORNEENSIS mollusc collection at Universiti Malaysia Sabah (BOR/MOL) resembling *Everettia*. We were able to exclude this *Everettia*-like material based on anatomical characteristics. Thus, this is a complete list of all *Everettia* spp. that can be found in Sabah, northern Borneo. Five previously established species are presented first, and are then followed by descriptions of all the new species. Almost all of the species have unique combinations of major characters (Table 1). A

dichotomous key to the Sabah species and subspecies of *Everettia* is therefore also provided.

Superfamily Dyakioidea Gude & Woodward, 1921
Family Dyakiidae Gude & Woodward, 1921
Subfamly Dyakiinae Gude & Woodward, 1921
Genus *Everettia* Godwin-Austen, 1891

Everettia Godwin-Austen, 1891 (type species: *Helix jucunda* Pfeiffer, 1863: 524, fig. 263a)

Type species: Helix jucunda Pfeiffer, 1863.

Nomenclature and systematics: Godwin-Austen (1891) proposed the genus *Everettia* to supplant five species in the genera *Helix*, *Macrochlamys*, and *Nanina* based on shell characters, namely, *Everettia consul*, *Everettia jucunda*, *Everettia hyalina*, *Everettia aglaja*, and *Everettia cutteri*. Moreover, eleven new species have been described since then: *Everettia subconsul* (Smith, 1887b); *Everettia subimperforata*, *Everettia planior*, *Everettia baramensis*, *Everettia bangueyensis*, and *Everettia thalia* (Smith, 1895); *Everettia pseustes* and *Everettia sanchesi* (Kobelt, 1905); *Everettia robusta* (Gude, 1917); *Everettia klemmantanica* (Gude, 1918); and *Everettia corrugata* (Laidlaw, 1937). Besides these species there were two species in the genus *Xesta* that probably belong to *Everettia*, namely, *Xesta themis* (Smith, 1895) and *Xesta padasensis* (Smith, 1895).

The genus *Everettia* seemed to be stabilized after Godwin-Austen (1891) and Smith (1895), but its taxonomic status was widely accepted only after Laidlaw (1931) included *Everettia* in the subfamily Dyakiinae, family Zonitidae. Fewer than half of the *Everettia* species had been described from Sabah, particularly in the west coast; the rest are known from Sarawak (Godwin-Austen, 1891; Smith, 1895; Von Martens & Thiele 1908).

Anatomically, the genus was found to be closely related to *Quantula striata* – the only representative species of this genus and absent from Borneo. However, the type of *Everettia* was described from north Borneo (Labuan Island, Sabah) and all the anatomically similar '*Everettia*' species were found in Borneo (Laidlaw, 1931). Thus, it appears that it is endemic to Borneo.

The anatomy of *Everettia jucunda* (?) (a specimen from Baram River, about 170 km south-west from the type locality, Labuan) including the muscles of the retractor system, the digestive system, circulation system, genitalia, and nervous system were described by Wiegmann (1898). The diagnostic characters for this genus separating it from other Dyakiinae, e.g. *Quantula*, *Dyakia*, *Kalamantania*, *Rhinocochlis*, *Bertia*, *Elaphroconcha*, *Sasakina*, and *Asperitas*, are the dart glands and dart-sac structures (Schileyko, 2003). *Everettia* has all of the numerous tubules embedded in the end of the dart-sac (Fig. 1A) whereas *Quantula*'s tubules of each accessory gland are fused into a single duct where it connects with the dart-sac (Baker, 1941; Schileyko, 2003). In addition, each of these tubules is connected with the accessory glands and lumped together but not packed by any outer layer or tissue as in *Phuphania* (Tumpeesuwan, Naggs & Panha, 2007) or *Everettia* (?) *mollendorffi* (Wiegmann, 1898).

The radula and exterior of the animal have almost no diagnostic value as these parts are very similar amongst genera in Dyakiinae (Fig. 1B; Godwin-Austen, 1891). The central tooth of the radula is tricuspid with two symmetrically placed outer small lateral cusps. The two outer cusps are asymmetrically placed where the position of the right cusp is lower than the left cusp and reduced to bicuspid for laterals toward the left margin of the radula and vice versa. The outermost marginal has lost both right and left lateral cusps. There are no linguiform shell-lobes on either the right or left side. Both right and posterior left mantle-lapplet are not projected, but the anterior left mantle-lapplet is slightly projected.

Everettia jucunda (Pfeiffer, 1863)

Helix jucunda Pfeiffer, 1863: 524, figure 263a.
Helix jucunda, Pfeiffer, 1867–1869: 307.
Nanina (Macrochlamys) jucunda, v. Martens, 1867: 240, plate 12, figure 7.
Nanina jucunda, Issel, 1874: 398.
Everettia jucunda, Godwin-Austen, 1891: 34–35, plate 3, fig. 1.
Everettia jucunda, Wiegmann, 1898: plate 23, figures 23–38.
Macrochlamys (Everettia) jucunda, Kobelt, 1905: 1014, plate 262, figures 6–7.
Everettia jucunda, Schileyko, 2003: 1360, figure 1775a.

Type material: BMNH 20040991, holotype (seen).

Material examined: SABAH – Tiga Islands: BOR/MOL 932, vii.2000, BOR/MOL 4237, v.2006, BOR/MOL 4261, ii.2006; JJ 11350, vii.2003; BMNH 1892.7.20.62.3. Labuan: BMNH 90.7.15.243-5; BMNH 2008216; BMNH 2008217; BMNH 2008218. Beaufort: ZMA 176861, Kuala Penyu, viii.1964. Sipitang: ZMA 176860, Sipitang beach, vii.1964; ZMA 176862, Sipitang beach, vii.1964. BRUNEI – Brunei: JJ 2493; JJ 10038, Labi Waterfall, iii.2003.

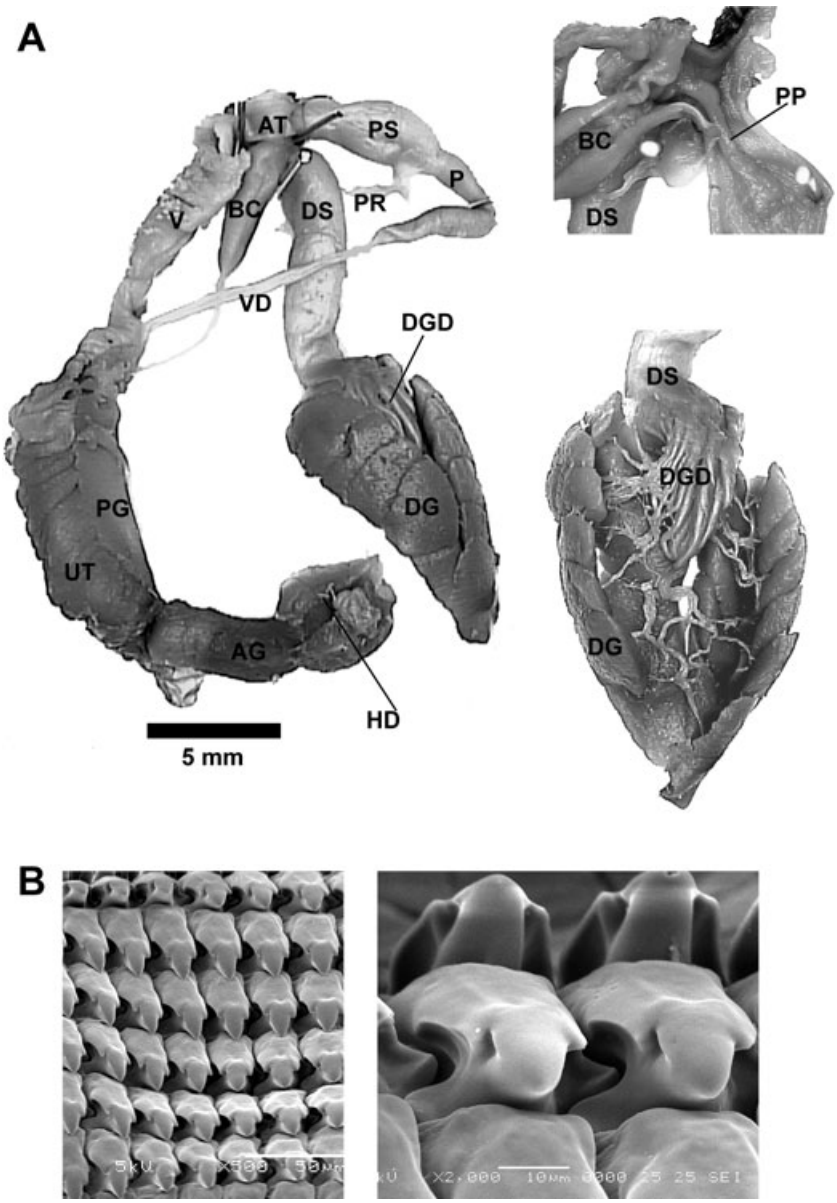

Figure 1. A, genitalia of *Everettia corrugata corrugata*, abbreviations: AG, albumen gland; AT, atrium; BC, bursa copulatrix; DG, dart-glands; DGD, dart-gland ducts; HD, hermaphroditic duct; P, penis; PG, prostate gland; PP, penial papilla; PR, penial retractor; PS, penial sheath; UT, uterus; V, vagina; VD, vas deferens; B, radula of *E. corrugata corrugata*.

Diagnostic characteristics: Upper shell dull with more spiral striation and more convex whorls compared with the shiny shell of *Everettia jucundior*.

Description: Shell (Figs 2D, 3B): medium-sized, rather thin, brownish, moderately elevated, outer whorls rounded. Periphery rounded. Above the periphery, shell shiny with a regularly and densely placed spiral striation, *c.* 30–40 per mm. Below the periphery, shell has fine, densely placed spiral grooves. Height up to 10.5 mm; width up to 17.3 mm; diameter of the first three whorls 0.8–0.9, 0.6–0.7, and 0.8–0.9 mm, respectively; number of whorls up to six and three-quarters; height aperture up to 7.7 mm; width aperture up to 9.8 mm. Genitalia: maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to *c*. 13 mm. P, V, GO, BC, and DS arranged around the short genital atrium, with limited space between the opening of each of the genital structures. Long BC almost same length as DS. Animal (Fig. 4C): black bands on either

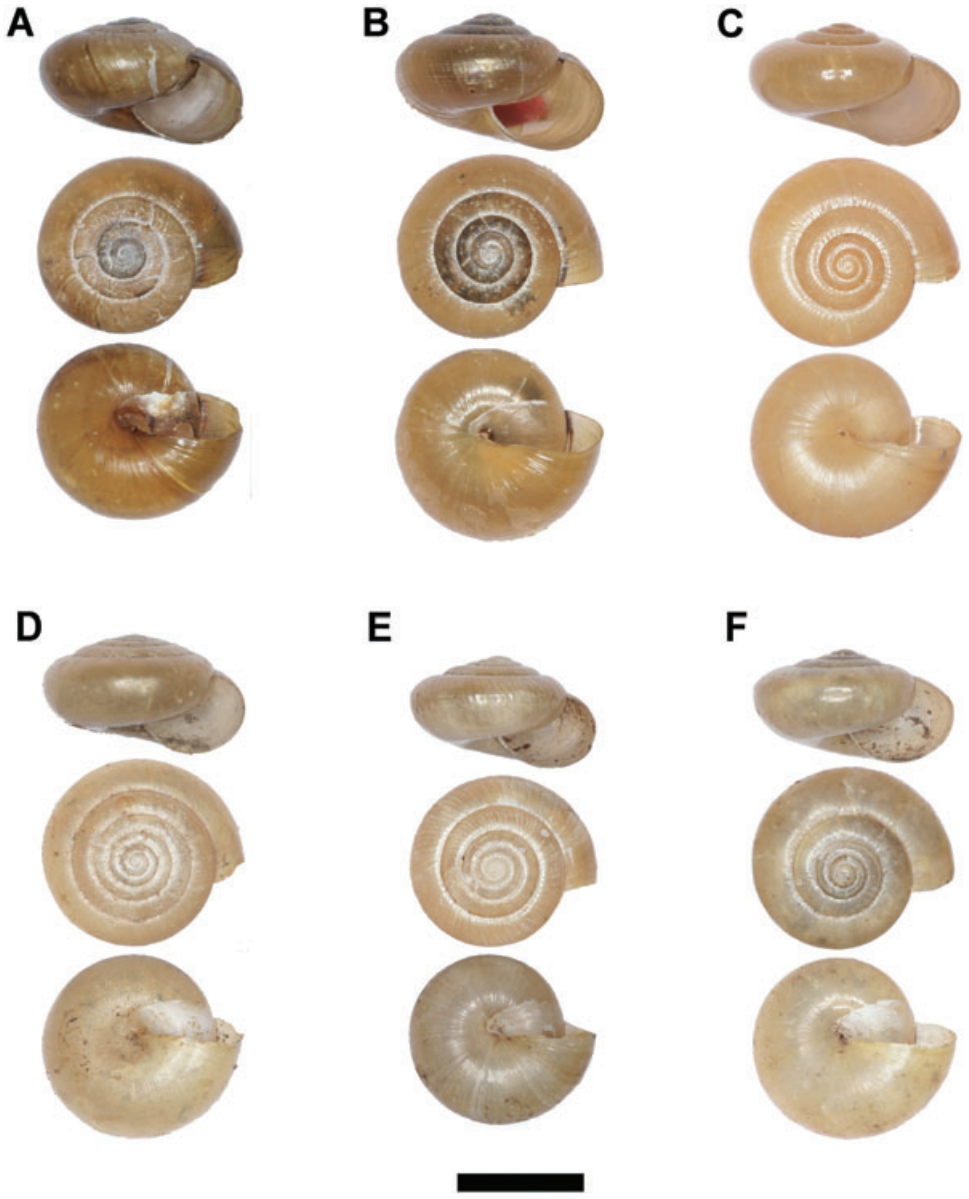

Figure 2. Shells. A, *Everettia corrugata corrugata*; B, ***Everettia corrugata williamsi* ssp. nov.**; C, ***Everettia interior* sp. nov.**; D, *Everettia jucunda*; E, ***Everettia occidentalis* sp. nov.**; F, ***Everettia jucundior* sp. nov.** Scale bar = 10 mm.

side of tentacles, which are divided by a white band occupying the space between eye tentacles, and extended backward to the end of mantle and downward to just below the eye tentacles. Grey smear on either side of the tail extending from the umbilicus region to the end of the tail. Other parts of the animal are devoid of any markings. The mantle is covered by brown irregular markings and followed by regularly spaced radial darker brown bands at the last half whorl.

Distribution and habitat: Primary forest and peat swamp forest. Sabah: Pulau Tiga, Beaufort, Klias Forest Reserve (Fig. 5A).

Remarks: The size of the specimens from Brunei is greater than the Beaufort and Pulau Tiga specimens. The type was described from Labuan Island, which is located at the centre of its known distribution range.

EVERETTIA SUBCONSUL (SMITH, 1887B)

Nanina subconsul, Smith, 1887b:132.
Macrochlamys subconsul, Smith, 1887a: 216, plate 9, figures 4–6.
Macrochlamys (Everettia) subconsul, Kobelt, 1905: 1011, plate 261, figures 8–10.
Xesta themis, Haas, 1951: 623, figure 131.

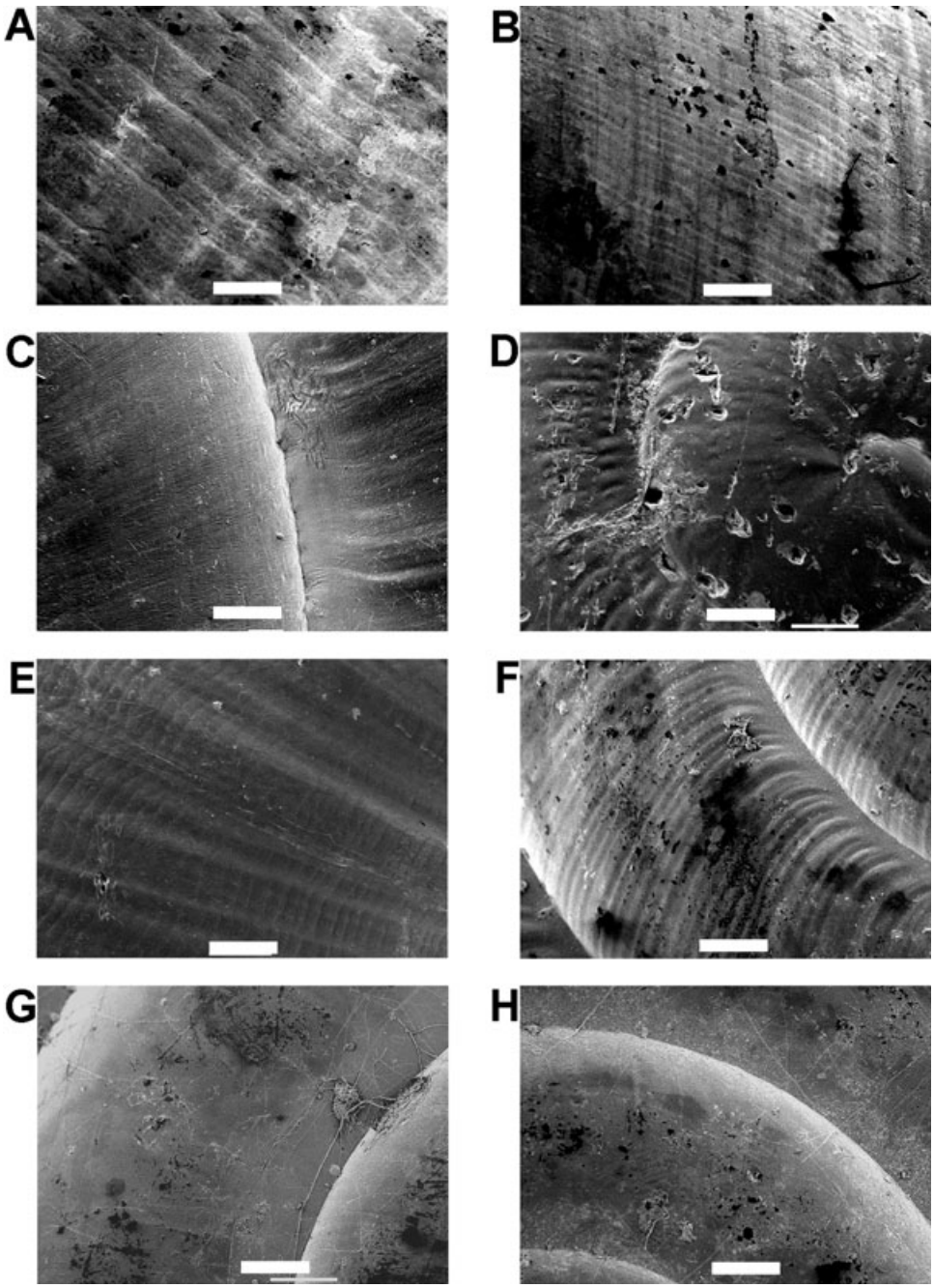

Figure 3. Shell surface sculptures (scanning electron micrograph). A, upper surface of ***Everettia interior* sp. nov.**; B, upper surface of *Everettia jucunda*; C, upper surface of ***Everettia layanglayang* sp. nov.**; D, protoconch of ***E. layanglayang* sp. nov.**; E, underside of ***E. layanglayang* sp. nov.**; F, upper surface of ***Everettia dominiki* sp. nov.**; G, upper surface of ***Everettia monticola* sp. nov.**; H, upper surface of ***Everettia planispira* sp. nov.** Scale bar = 200 μm.

Type material: BMNH 1889.5.21.1, holotype (seen).

Material examined: SABAH – Imbak Valley: BOR/MOL 925, vi.2000; BOR/MOL 5272, vi.2006. Meliau Range: BOR/MOL 3186, 355 m altitude (alt.), viii.2004; BOR/MOL 3187, 100 m alt., viii.2004; BOR/MOL 3188, 150 m alt., viii.2004; BOR/MOL 3190, 150 m alt., viii.2004; BOR/MOL 3191, 640 m alt., viii.2004; BOR/MOL 3192, 650 m alt., viii.2004; BOR/MOL 5263, 355 m alt., viii.2004; BOR/MOL 5266,

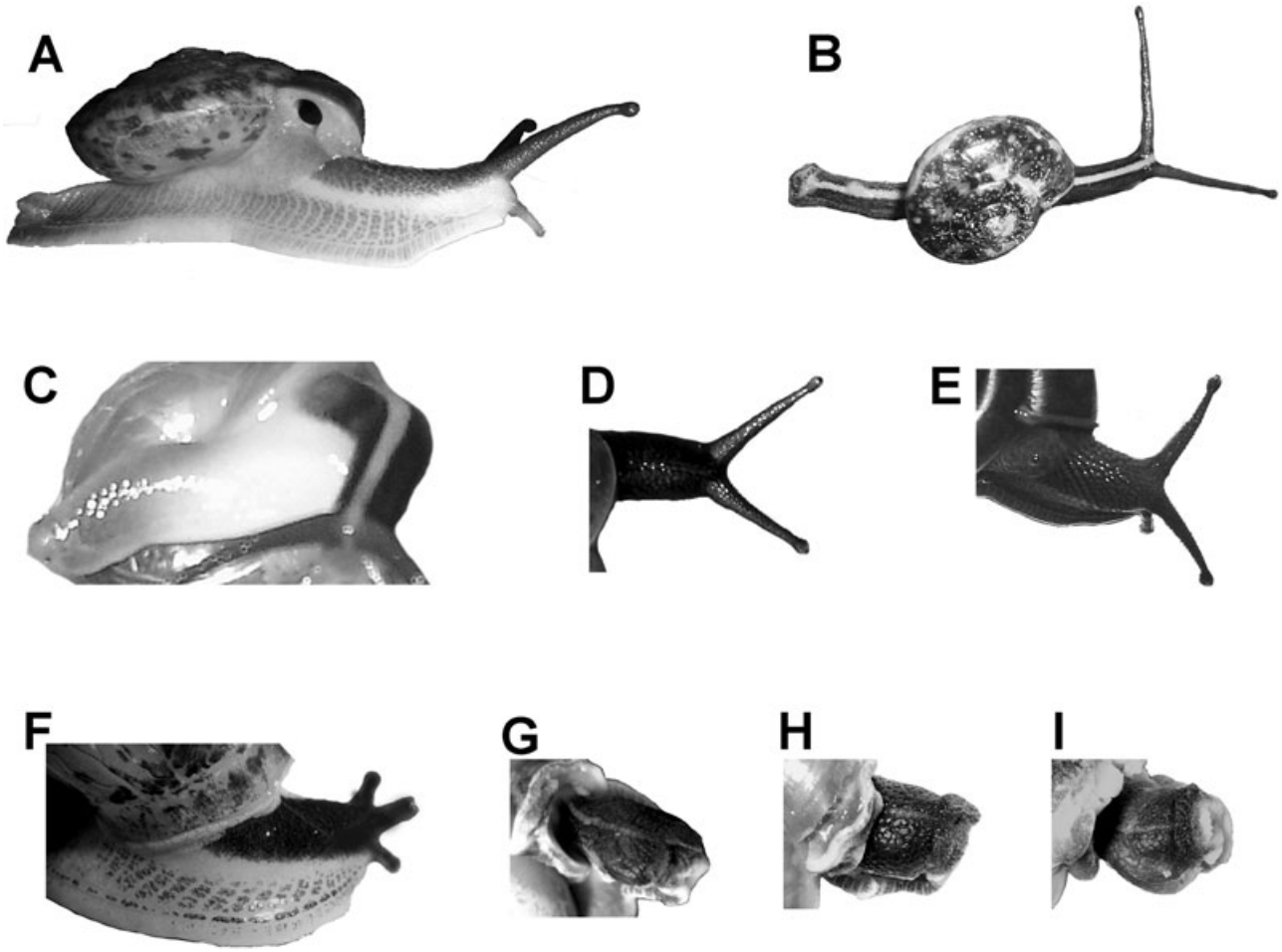

Figure 4. Animal head and body pigmentation. A, *Everettia klemmantanica*; B, ***Everettia interior* sp. nov.**; C, *Everettia jucunda*; D, *Everettia themis*; E, ***Everettia layanglayang* sp. nov.**; F, *Everettia subconsul*; G–I, possible hybrid of *E. themis* and *E. subconsul*.

470 m alt., viii.2004. Danum Valley: BOR/MOL 931, iii.2001; BOR/MOL 936, ix.2000; BOR/MOL 937, iii.2001; BOR/MOL 938, ix.2002; BOR/MOL 943, v.2000; BOR/MOL 947, v.2000; BOR/MOL 948, vii.2001; BOR/MOL 952, v.2000; BOR/MOL 953, v.2000; BOR/MOL 963, v.2000; BOR/MOL 965, vii.2001; BOR/MOL 970, iii.2001; BOR/MOL 974, ix.2000; BOR/MOL 1231, v.2000; BOR/MOL 4250, vi.2006; BOR/MOL 4781, ix.2000; BOR/MOL 4889, iii.2001; BOR/MOL 5119, iii.2000; BOR/MOL 5393, vii.2001; JJ 1197, ix.1986. Tabin Wildlife Reserve: BOR/MOL 5230, v.2001. Crocker Range: BOR/MOL 933, 1420 m alt., x.2000; BOR/MOL 1374, Kimanis, 300 m alt., ix.2002; BOR/MOL 1424, Ulu Kimanis, 750 m alt., ix.2002; BOR/MOL 1378, Ulu Kimanis, 1200 m alt., vi.2003; BOR/MOL 3112, Melalap, 480 m alt., i.2004; BOR/MOL 3362, Inobong, xi.2004; BOR/MOL 5240, Sugud Forest Reserve, vi.2003; BOR/MOL 5262, Kg. Langsat, 200 m alt., vi.2004; BOR/MOL 935, Kiansom, i.2001; BOR/MOL 972, Kiansom, xii.2000; BOR/MOL 3479, Kiansom, iii.2005; BOR/MOL 4813, Kiansom, xii.2000; BOR/MOL 949, Mahua, 1200 m, vii.2001; SP 12214, Ulu Megindanau, 130 m alt. ix.2002; SP 12453, Ulu Liawan, ix.2005 SP 12524, Melangkap Tomis, v.2005; SP 12593, Ulu Kimanis, ix.2005; SP 12648, Ulu Kimanis, ix.2005; SP 12651, Ulu Kimanis, ix.2005; SP 12804, Nalapak, x.2006; SP 12709, Ulu Membakut, ii.2006; SP 12784, Ulu Kimanis, iv.2006. Kinabatangan: BOR/MOL 1291, Bod Tai, 100 m alt., v.2002; BOR/MOL 1295, Keruak, 50 m alt., iv.2002; BOR/MOL 1296, Ulu Sungai Resang, i.2003; BOR/MOL 1377, Pangi, 100 m alt., v.2002; BOR/MOL 1387, Batu Tomanggong Besar, 50 m alt., iv.2002; BOR/MOL 1388, Pangi, 100 m alt., v.2002; BOR/MOL 1394, Batu Tomanggong Besar, 50 m alt., iv.2003; BOR/MOL 2084, Batu Materis, 36 m alt., iv.2003; BOR/MOL 2304, Batu Keruak, 43 m alt., iii.2003; BOR/MOL 2305, Batu Tai,

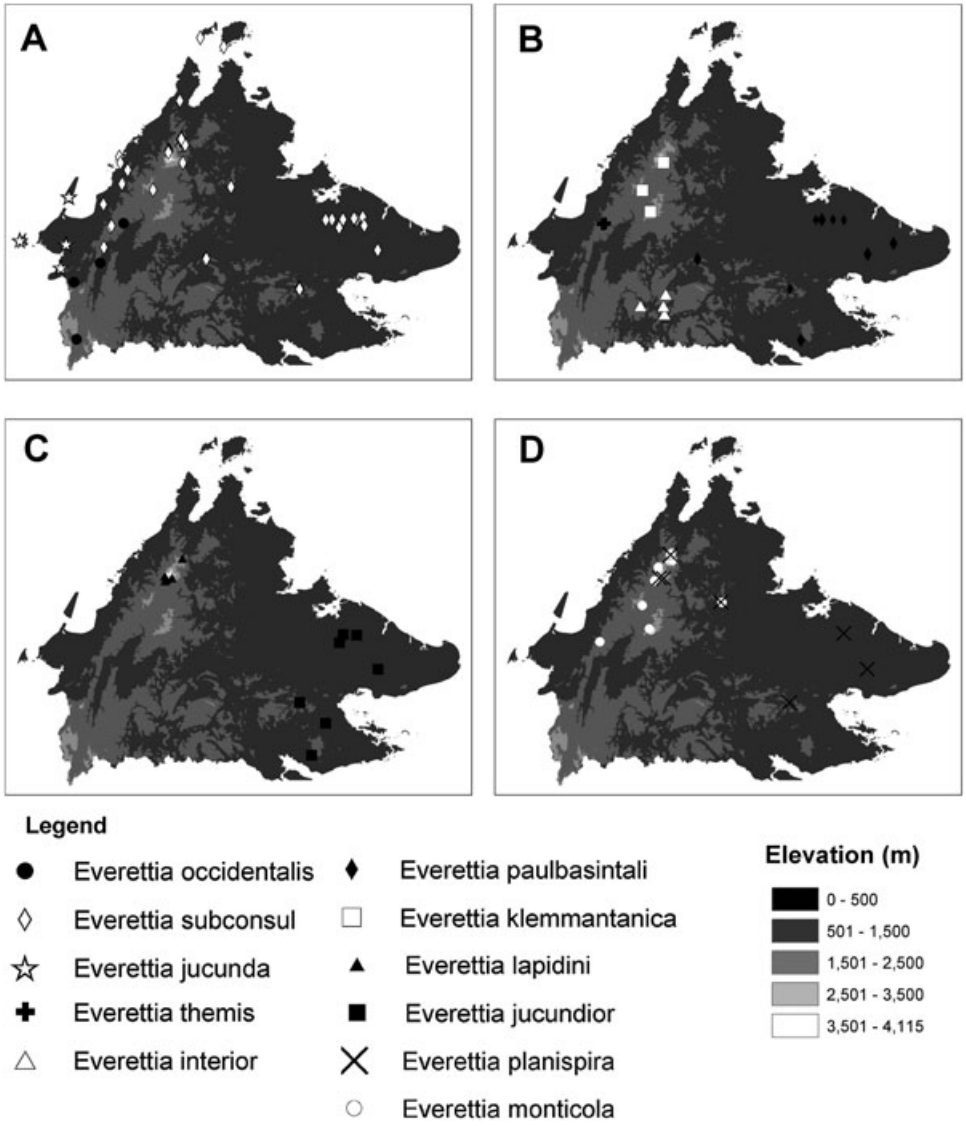

Figure 5. Distribution maps (Sabah). A, *Everettia subconsul* in the east and west coast lowland, *Everettia jucunda* in the west coast, and ***Everettia occidentalis* sp. nov.** in the western mountain range; B, *Everettia klemmantanica* in the central mountain ranges, ***Everettia interior* sp. nov.** in the interior area, ***Everettia paulbasintali* sp. nov.** in the east coast lowland, *Everettia themis* in the central mountain ranges; C, ***Everettia lapidini* sp. nov.** in the central mountain ranges, ***Everettia jucundior* sp. nov.** in the east coast lowland; D, ***Everettia monticola* sp. nov.** in the central mountain ranges, ***Everettia planispira* sp. nov.** in the eastern and northern parts of Sabah.

70 m alt., iii.2003; BOR/MOL 2306, Bukit Mawas, 14 m alt., iii.2003; BOR/MOL 2307, Bukit Mawas, 30 m alt., iii.2003; BOR/MOL 2308, Batu Materis, 36 m alt., iv.2003; BOR/MOL 2309, Sukau, 50 m alt., iii.2003; BOR/MOL 2311, Batu Tomanggong Besar, 50 m alt., viii.2003; BOR/MOL 2312, Batu Tomanggong Besar, 50 m alt., viii.2003; BOR/MOL 2491, Bukit Mawas, 14 m alt., iii.2003; BOR/MOL 3646, Gomantong, xii.2004; JJ 9576, Bod Tai, iv.2002; JJ 9612, Tandu Batu, 20 m alt., iv.2002; JJ 9658, Batu Pangi, 20 m alt., iv.2002; JJ 9672, Batu Pangi, 20 m alt., iv.2002. Kota Kinabalu: BOR/MOL 915, Gaya Island, vii.2001; BOR/MOL 1305, Universiti Malaysia Sabah; BOR/MOL 3370, Karambunai, i.2004. Kudat: BOR/MOL 3009, Banggi Island, 50 m alt., 2003; BOR/MOL 3686, Balambangan Island, v.2005; BOR/MOL 4375, Kg. Magnin, 239 m alt., vii.2006; JJ 9507, Balambangan Island, iv.2002; JJ 9534, Balambangan Island, iv.2002. JJ 9545, Balambangan Island, iv.2002; BMNH 1893.6.8.59–60, Banggi Island, 1893; BMNH 1893.6.7.13, Banggi Island, 1893. Mount Kinabalu: BOR/MOL 3114, Serinsim, 200 m alt.,

2004; BOR/MOL 940, Poring, 660 m alt., xi.2001; BOR/MOL 1385, Sayap, 1000 m alt., x.2002; BOR/MOL 4421, Sayap, 1152 m alt., xi.2005; BOR/MOL 4423, Sayap, 1496 m alt., xi.2005; SP 12537, western slope, Sayap substation, v.2005; SP 12658, western slope, Sayap substation, xi.2005; SP 12802, western slope, Sayap substation, ix.2006; SP 12828, western slope, Sayap substation, x.2006; ZMA 176864, 1920. Mount Tambuyukon: BOR/MOL 4409, eastern slope, 896 m alt., x.2005; BOR/MOL 4416, eastern slope, 1016 m alt., x.2005; BOR/MOL 4425, eastern slope, 1144 m alt., x.2005; BOR/MOL 4428, eastern slope, 880 m alt., x.2005; SP 12491, north-eastern slope, iv.2005. Mount Nombuyukon: BOR/MOL 4410, north-eastern slope, 1070 m alt., xi.2005; BOR/MOL 4411, north-eastern slope, 548 m alt., xi.2005; BOR/MOL 4413, north-eastern slope, 452 m alt., xi.2005; BOR/MOL 4414, north-eastern slope, 1204 m alt., xi.2005; BOR/MOL 4415, north-eastern slope, xi.2005; BOR/MOL 4417, north-eastern slope, 1380 m alt., xi.2005; BOR/MOL 4418, north-eastern slope, xi.2005; BOR/MOL 4419, xi.2005; BOR/MOL 4420, north-eastern slope, 877 m alt., xi.2005; BOR/MOL 4422, north-eastern slope, 700 m alt., xi.2005; BOR/MOL 4424, north-eastern slope, 1001 m alt., xi.2005; BOR/MOL 4426, north-eastern slope, xi.2005. Telupid: JJ 1263, Mount Tawai, xi.1986.

Diagnostic characteristics: This is a smooth-shelled species with its mantle covered by regularly spaced radial darker brown bands at the last half whorl. All the other species with similar mantle markings from Sabah have distinct sculpture above the periphery. *Everettia subconsul* differs from *Everettia layanglayang* in animal colour and mantle markings.

Description: Shell (Fig. 6C): large, rather thin, yellowish brown. Spire moderately to distinctly elevated, outer whorls slightly shouldered below the suture. Periphery slightly shouldered to almost rounded, more distinctly angular in juveniles. Above the periphery, shell silky with very weak (but distinct) oblique wrinkling, slightly stronger towards the suture. Amongst this wrinkling, very fine granulation [40× magnification (magn.)] is arranged obliquely, sometimes with inconspicuous spaced spiral grooves. Below the periphery, shell has fine, densely placed spiral grooves. Height up to 18 mm; width up to 32.5 mm; diameter of each of the first three whorls is 0.9–1.0 mm; number of whorls up to six and a half; height aperture up to 12.5 mm; width aperture up to 15.5 mm. Width : height ranges from 1.63 to 1.76 (Danum) or 1.75 to 1.90 (Kinabatangan). Genitalia (Fig. 7D): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 16 mm. The penis, dart-sac, and vagina very thin with thick muscular wall. P, V, GO, BC, and DS arranged around the short genital atrium, with limited space between the opening of each of the genitalia structures. Short BC about one-quarter to one-third of total DS length. Animal (Figs 4F, 8A, F): black bands on either side of tentacles, which are divided by a white band that occupies the space between eye tentacles, and extends backward to the end of mantle and downward to just below the eye tentacles. Other parts of the animal are covered by regularly spaced oblique dotted belts. The mantle is covered by brown irregular markings and followed by regularly spaced radial darker brown bands at the last half whorl.

Distribution and habitat: Primary forest, up to 1400 m alt. Sabah: west coast, east coast, and interior area. Danum Valley, Kinabatangan, Crocker Range, Pulau Banggi, Kota Kinabalu (Figs 5A, 9D).

Remarks: Some of the immature specimens from this species have a keeled shell as does *Everettia themis*, but *Everettia subconsul* has a more rounded lower periphery than *E. themis*. The populations in the interior of Sabah, the west coast, and at higher elevations have a small and rounded-periphery shell. It is not possible to differentiate the typical lowland *E. subconsul* and highland *Everettia layanglayang* from the shell alone. Nevertheless, we decided that the type specimen of *E. subconsul* is identical to the *Everettia* species that is common throughout the lowlands of Sabah. The type locality – north Borneo, had not been specified by either Whitehead (1893) or Smith (1887b). According to the report of Whitehead (1893), the attempt to climb Mount Kinabalu was not successful until the end of January 1888. The type was collected by Whitehead during his Exploration of Mount Kinabalu between 1885 and 1887; and described by Smith (1887b). Thus, we presume that the type specimen was collected during his second failed attempt to Mount Kinabalu, in the Melangkap area where the elevation does not exceed 1200 m. However, *E. layanglayang* can only be found above 1800 m.

EVERETTIA THEMIS (SMITH, 1895)

Xesta themis (Smith, 1895: 100), plate 2, figures 1, 2.
Nanina (*Xestina*) *themis*, Kobelt (1905: 994), plate 257, figures 10, 11.

Type material: BMNH 1894.7.21.112/1894.7.203-4, Holotype (seen).

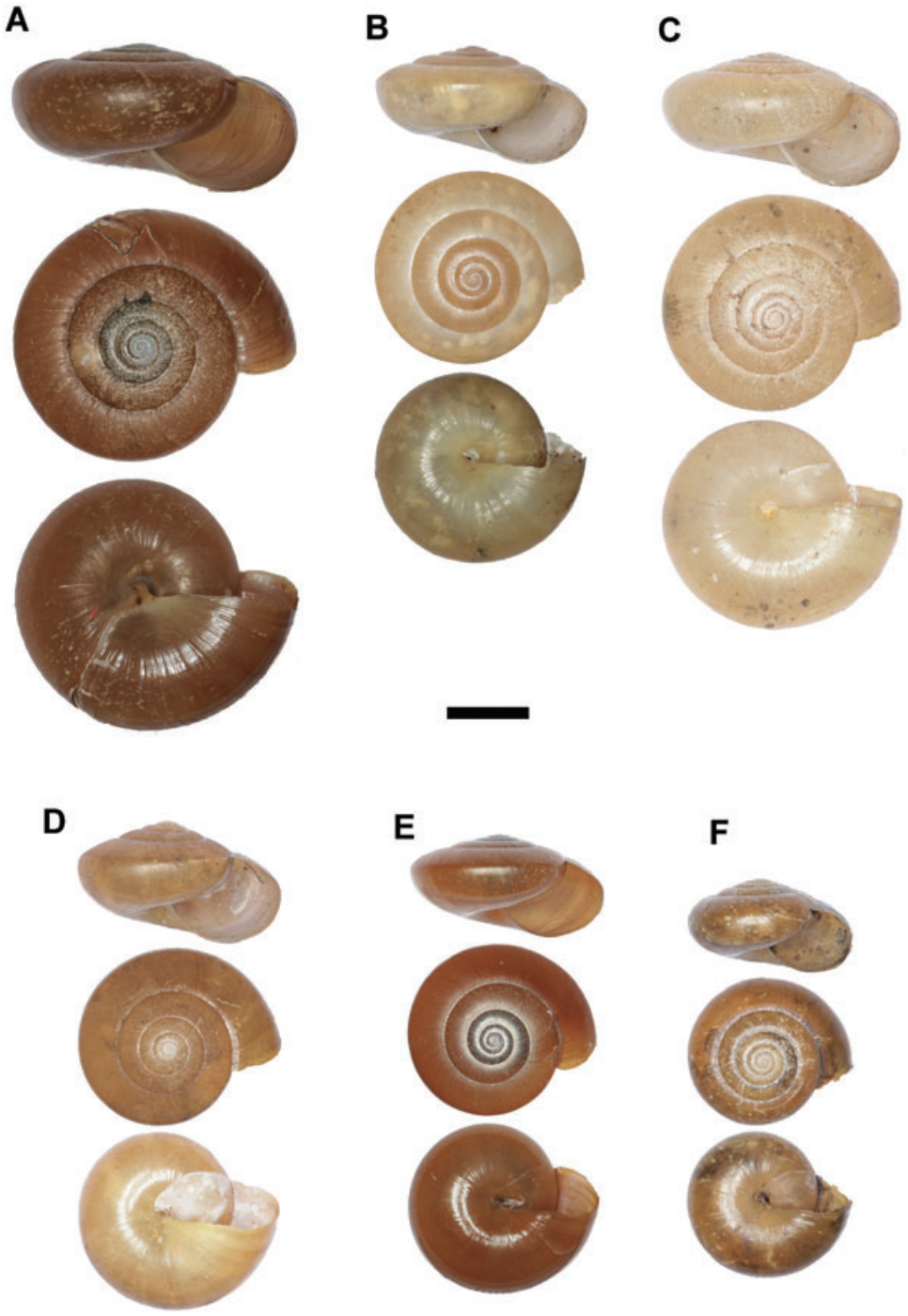

Figure 6. Shells. A, ***Everettia lapidini* sp. nov.**; B, *Everettia klemmantanica*; C, *Everettia subconsul*; D, ***Everettia paulbasintali* sp. nov.**; E, *Everettia themis*; F, ***Everettia layanglayang* sp. nov.** Scale bar = 10 mm.

Material examined: SABAH – Crocker Range: SP 12599, Ulu Kimanis, ix.2005; SP 12788, Ulu Kimanis, iv.2006. Mount Kinabalu: SP 12359, Bundu Tuhan Trail, xii.2003; SP 12360, Bundu Tuhan Trail, xii.2003; SP 12813, Bundu Tuhan Trail, vii.2006; BMNH 20080215, southern slope, 2000 m alt., 1967.

Diagnostic characteristics: This species is easily recognized by its reddish keeled shell (for the Crocker range population) or brown rounded-periphery shell (for the Mount Kinabalu population) and uniform black animal.

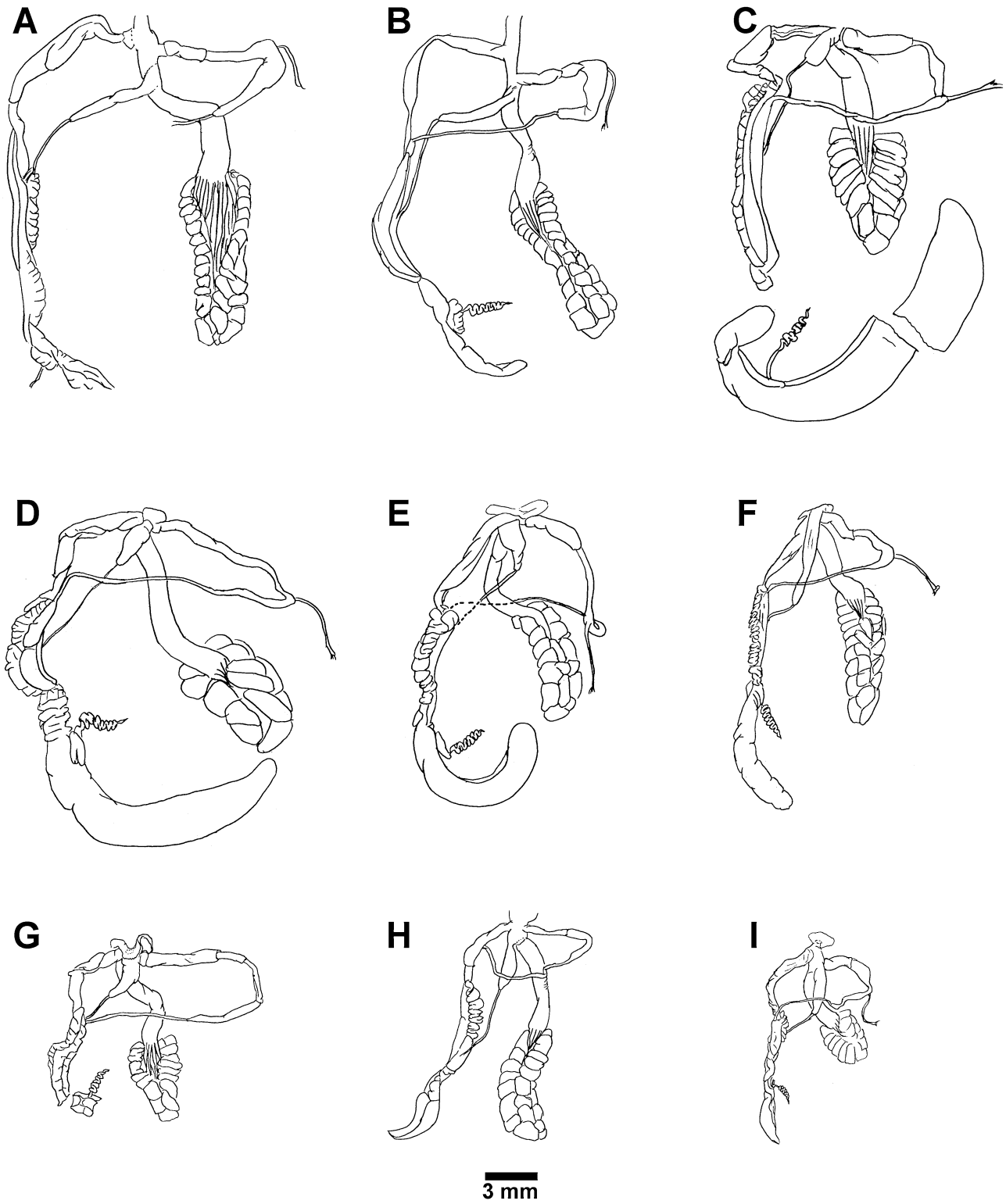

Figure 7. Genitalia. A, *Everettia klemmantanica*; B, ***Everettia lapidini* sp. nov.**; C, ***Everettia paulbasintali* sp. nov.**; D, *Everettia subconsul*; E, *Everettia themis*; F, ***Everettia layanglayang* sp. nov.**; G, ***Everettia jucundior* sp. nov**.; H, ***Everettia interior* sp. nov.**; I, *Everettia corrugata corrugata*.

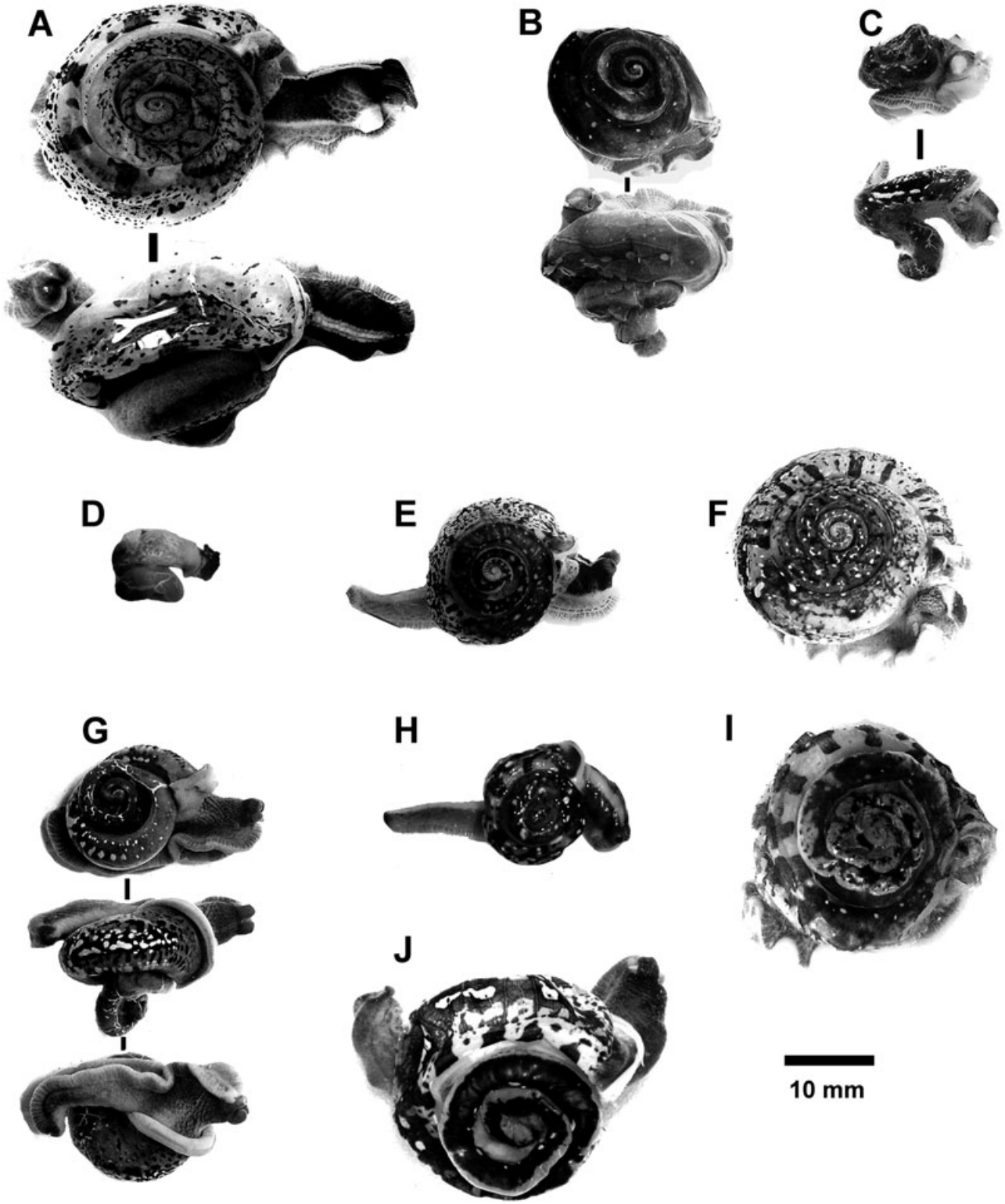

Figure 8. Animal and mantle pigmentation. A, *Everettia subconsul* west coast lowland; B, ***Everettia layanglayang* sp. nov.**; C, ***Everettia monticola* sp. nov.**; D, ***Everettia safriei* sp. nov.**; E, ***Everettia interior* sp. nov.**; F, *Everettia subconsul* east coast lowland; G, *Everettia corrugata corrugata*; H, ***Everettia jucundior* sp. nov.**; I, *Everettia klemmantanica*; J, ***Everettia lapidini* sp. nov.**

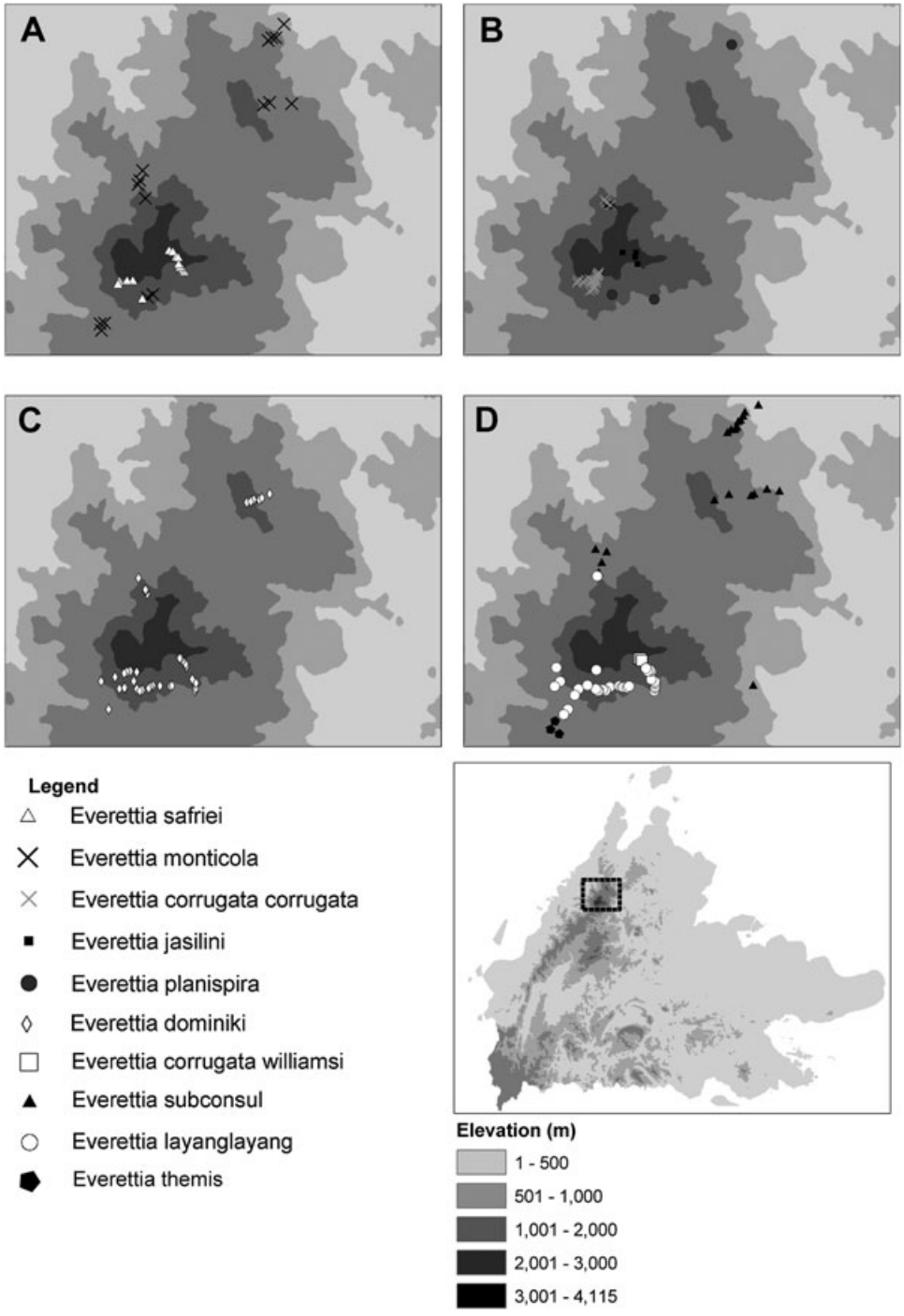

Figure 9. Distribution maps (Mount Kinabalu and Mount Tambuyukon). A, ***Everettia monticola* sp. nov.** and ***Everettia safriei* sp. nov.**; B, ***Everettia planispira* sp. nov.**, ***Everettia jasilini* sp. nov.**, and *Everettia corrugata corrugata*; C, ***Everettia dominiki* sp. nov.**; D, *Everettia themis*, *Everettia subconsul*, ***Everettia corrugata williamsi* ssp. nov.** and ***Everettia layanglayang* sp. nov.**

Description: Shell (Fig. 6E): large, rather thin, reddish brown, or brown. Spire moderately elevated, outer whorls shouldered below the suture. Periphery angular to round. Above the periphery, shell silky with very weak (but distinct) oblique wrinkling, slightly stronger towards the suture. Amongst this wrinkling, very fine granulation (40× magn.) is arranged obliquely. Below the periphery, shell has

fine, densely placed spiral grooves. Height up to 12.0 mm; width up to 22.0 mm; diameter of the first three whorls 1.0–1.1, 0.8–0.9, and 1.4–1.6 mm, respectively; number of whorls up to five and one-eighth; height aperture up to 9.3 mm; width aperture up to 11.6 mm. Genitalia (Fig. 7E): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 13 mm. The penis, dart-sac, and vagina very thin with thick muscular walls. P, V, GO, BC, and DS arranged around the short genital atrium, with limited space between the opening of each of the genital structures. Short BC about one-quarter to one-third of total DS length. Animal (Fig. 4D): animal head uniform black and this coloration extends backward to the end of the mantle and downward to the foot-fringe. Grey smear on other parts of animal extending to the end of the tail. The mantle is covered by brown irregular markings and followed by regularly spaced radial dark bands at the last half whorl.

Distribution and habitat: Primary lower montane forest. Sabah: Crocker Range (Ulu Kimanis = 1400–1800 m alt. and Mount Kinabalu = 1400–1900 m alt.) and Upper Padas River (old record) (Figs 5B, 9D).

Remarks: The type locality is Upper Padas, north Borneo, but the exact elevation and location is unknown. All the recent material was found at Upper Kimanis and Mount Kinabalu between 1400 and 1900 m, which is at least 70 km in a direct line north-east from the type locality.

EVERETTIA KLEMMANTANICA GUDE, 1918

Everettia klemmantanica Gude, 1918: 19–20.

Type material: BMNH 1922.8.29.19, Holotype (seen).

Material examined: SABAH – Crocker Range: BOR/MOL 1292, Mahua, 1000 m alt., iii.2002; BOR/MOL 1307, Mahua, 1000 m alt., vii.2001; BOR/MOL 3608, Mahua, 1000 m alt., iv.2005; JJ 9721, Mahua, iv.2002.

Diagnostic characteristics: The densely placed nodules over the surface and more angular periphery distinguish this species from *E. paulbasintali* and the others.

Description: Shell (Figs 6B, 10F, H): large, rather thin, yellowish brown. Spire moderately elevated, outer whorls shouldered below the suture. Periphery slightly angular, more distinctly angular in juveniles. Above the periphery, shell with a silky lustre, very densely placed radial riblets, and cut by very densely arranged spiral grooves, forming nodules over the surface. Below the periphery, shell has fine, densely placed spiral grooves. Height up to 15.4 mm; width up to 30.8 mm; diameter of the first three whorls 1.3–1.5, 0.9–1.1, and 1.9–2.0 mm, respectively; number of whorls up to five and seven-eighths; height aperture up to 11.1 mm; width aperture up to 15.8 mm. Genitalia (Fig. 7A): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 18 mm. The penis, dart-sac, and vagina with thick muscular walls. P, V arranged near the GO then followed by BC and DS where there is much space in the atrium between the openings of P + V and BC + DS. Long BC about two-thirds of total DS length. Animal (Figs 4A, 8I): lighter black bands on either side of tentacles, which are divided by a white band that occupies the space between eye tentacles, and black bands faded towards the end of mantle and downward to just below the eye tentacles. Other parts of the animal are covered by regularly spaced oblique dotted belts. The mantle is almost uniformly reddish brown and followed by regularly spaced radial darker brown bands at the last half whorl.

Distribution and habitat: Primary forest, 1200–1800 m alt. Sabah: Crocker Range – Mahua and Mesilau (Fig. 5B).

Remarks: The type materials were obtained from a natural history dealer in 1904 (Gude, 1918). Type locality was in Borneo with unknown exact location.

EVERETTIA CORRUGATA CORRUGATA LAIDLAW, 1937

Everettia corrugata Laidlaw, 1937: 179–180, plate 11, figures 1, 2.

Everettia corrugata, Schileyko, 2003: 1360, figure 1775b, c.

Type material: BMNH 1936.6.16.1, holotype (seen).

Material examined: SABAH – Mount Kinabalu: BOR/MOL 941, southern slope, 3200 m alt., xi.2001; BOR/MOL 2679, southern slope, 3080 m alt., ix.2003; BOR/MOL 2688, southern slope, 2865 m alt., ix.2003; BOR/MOL 2866, southern slope, 3330 m alt., x.2003; BOR/MOL 2869, southern slope, 3080 m alt., ix.2003; BOR/MOL 2874, southern slope, 2865 m alt., ix.2003; BOR/MOL 2996, southern slope, 2700 m alt., x.2003; BOR/MOL 5275, southern slope, 3270 m alt., i.2005; BOR/MOL 5276, southern slope, 2800 m alt., ix.2005; BOR/MOL 5277, southern slope, 2944 m alt., xi.2005; BOR/MOL 5278, southern slope, 2896 m alt., xii.2004; BOR/MOL 5279, southern slope, 3088 m alt., ix.2005; BOR/MOL 5281, southern slope, 2911 m alt., xii.2004; BOR/MOL

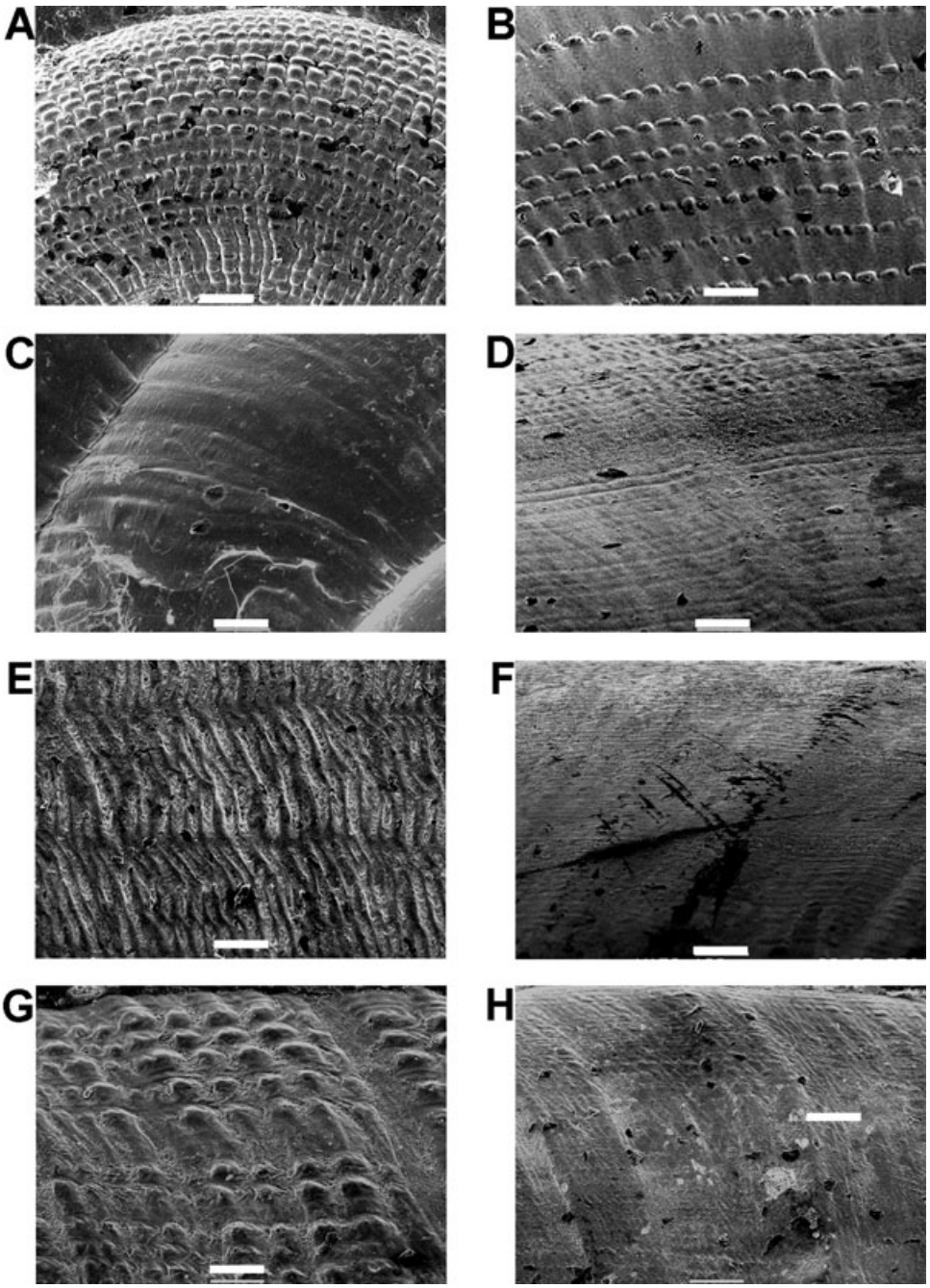

Figure 10. Shell surface sculptures (scanning electron micrographs). A, upper surface of ***Everettia jasilini* sp. nov.**; B, underside of ***E. jasilini* sp. nov.**; C, upper surface of ***Everettia safriei* sp. nov.**; D; underside of ***Everettia paulbasintali* sp. nov.**; E, upper surface of ***E. paulbasintali* sp. nov.**; F, underside of *Everettia klemmantanica*; G, upper surface on the fourth whorl of *E. klemmantanica*; H, upper surface on the second whorl of *E. klemmantanica*. Scale bar = 100 μm.

5282, southern slope, 3098 m alt., xii.2004; BOR/MOL 5283, southern slope, 3290 m alt., i.2005; BOR/MOL 5284, southern slope, 3211 m alt., i.2005; BOR/MOL 5285, southern slope, 2800 m alt., ix.2005; BOR/MOL 5286, southern slope, 3024 m alt., ix.2005; BOR/MOL 5287, southern slope, 3088 m alt., ix.2005; BOR/MOL 5288, southern slope, 2775 m alt., xii.2004; BOR/MOL 5289, southern slope, 3154 m alt., i.2005; BOR/MOL 5290, southern slope, 3304 m alt., i.2005; BOR/MOL 5293, southern slope, 2896 m alt., ix.2005; BOR/MOL 5294, southern slope, 3221 m alt., i.2005; BOR/MOL 5291, southern

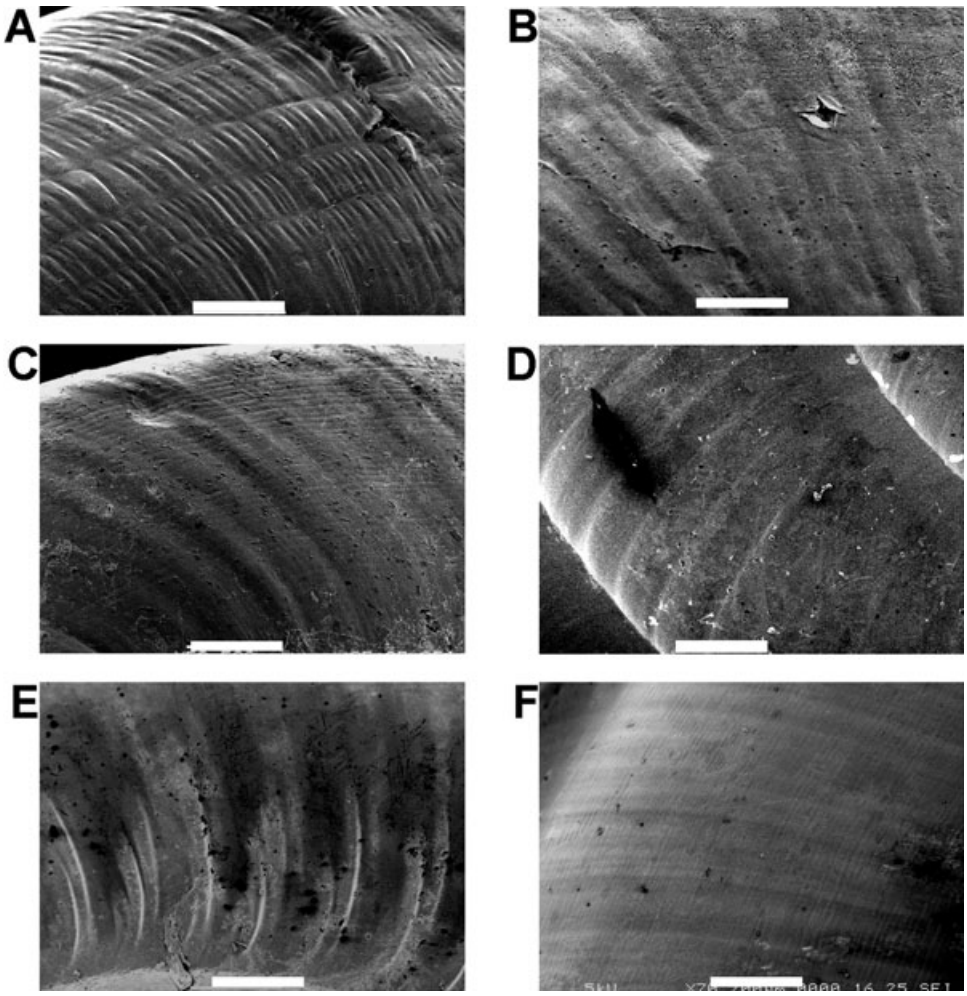

Figure 11. Shell surface sculptures (scanning electron micrographs). A, upper surface of ***Everettia corrugata williamsi* ssp. nov.**; B, underside of ***E. corrugata williamsi* ssp. nov.**; C, underside of *Everettia lapidini*; D, upper surface of ***Everettia occidentalis* sp. nov.**; E, corrugation at the suture of *Everettia corrugata corrugata*; F, upper surface of ***Everettia jucundior* sp. nov.** Scale bar = 500 μm.

slope, 2578 m alt., xi.2005; BOR/MOL 5292, southern slope, 3008 m alt., xi.2005; BOR/MOL 5280, southern slope, 2640 m alt., xi.2005. BOR/MOL 2672, southern slope, 3333 m alt., x.2003; JJ 4085, southern slope, Paka, 3000 m alt., iv.2004; JJ 5953; SP 12107, southern slope, 2600 m alt., x.2000; SP 12108, southern slope, 2600 m alt., x.2000; SP 12109, southern slope, 2600 m alt., x.2000; SP 12323, southern slope, Liwaagu trail, i.2004; SP 12338, southern slope, Paka, 3000 m alt., iv.2004; SP 12511, southern slope, 2600 m alt., vii.2005; SP 12568, southern slope, Silau-silau, vii.2005; SP 12659, southern slope, 2600 m alt., xi.2005; SP 12666, southern slope, 2600 m alt., xi.2005; SP 12670, southern slope, 2600 m alt., xi.2005; SP 12837, southern slope, 2600 m alt., xi.2005; SP 12947, southern slope, Maraiparai, v.2007. BMNH 20080211, southern slope, 3000 m alt.; BMNH 20080212, southern slope, 2600 m alt., viii.1967; BMNH 20080213, southern slope, 2600 m alt., viii.1967; ZMA 176868, southern slope, 3000 m alt., viii.1937.

Diagnostic characteristics: Very strong corrugation near the suture.

Description: Shell (Figs 2A, 11E): medium-sized, rather thin, greenish brown, moderately to distinctly elevated, outer whorls slightly shouldered below the suture. Periphery rounded. Above the periphery, shell shiny with very weak and irregular wrinkling that grows stronger towards suture, and forms corrugation just below the suture. Below the periphery, shell without or with scattered, inconspicuous, fine spiral grooves. Height up to 11.9 mm; width up to 19.6 mm;

diameter of the first three whorls 1.3–1.4, 1.1–1.2, and 1.85–2.3 mm, respectively; number of whorls up to five; height aperture up to 7.4 mm; width aperture up to 10.7 mm. Genitalia (Fig. 7I): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 11.5 mm. The penis, dart-sac, and vagina with thick muscular walls. P, V arranged near the GO then followed by BC and DS where there is little space in the atrium between the openings of P + V and BC + DS. Long BC about two-thirds of total DS length. Animal (Fig. 8G): animal head uniform black or grey and this colour extends backward to the end of mantle and downward to the foot-fringe. Some individuals with an ill-defined grey band between tentacles, extended to the end of the tail. Grey smear covering large parts of the animal and extending until the end of the tail. The mantle is covered in sparsely distributed brighter spots. These brighter spots become denser and are agglomerated with the black spots at the last half whorl.

Distribution and habitat: Upper montane and coniferous primary forest, 2500–3500 m alt. Sabah: Mount Kinabalu only (Fig. 9B).

Remarks: This species is endemic to Mount Kinabalu.

EVERETTIA CORRUGATA WILLIAMSI SSP. NOV.

Types: MALAYSIA: State of Sabah: Ranau District. Southern part of Kinabalu Park. At 3100 m alt. along Kotal's route from Bukit Babi to eastern ridge of Mount Kinabalu (6°4′N, 116°36′E). Collected by T.-S. Liew, J. Lapidin, Safrie, and Jasilin. Date: 23.iv.2005; holotype, BOR/MOL 5297, Figure 2B; four paratypes, two in BMNH 20080625 and two in SP 13057.

Etymology: This species is named after Dr Peter Williams (Oxford), who did the first malacological survey for Mount Kinabalu's eastern ridges during the Cambridge Kinabalu Expedition in 1967.

Material examined: SABAH – Mount Kinabalu: BOR/MOL 5295, eastern slope, 2812 m alt., iv.2005; BOR/MOL 5296, eastern slope, 2676 m alt., iv.2005; BOR/MOL 5298, eastern slope, 2992 m alt., iv.2005; BOR/MOL 5299, eastern slope, 3064 m alt., iv.2005; BOR/MOL 5300, eastern slope, 2280 m alt., iv.2005.

Diagnostic characteristics: Shell above with regularly and densely placed radial threads and cut by widely spaced spiral grooves.

Description: Shell (Figs 2B, 11A, B): medium-sized, rather thin, greenish brown, moderately to distinctly elevated, outer whorls slightly shouldered below the suture. Periphery rounded. Above the periphery, shell with a silky lustre, regularly and densely placed, distinct radial threads and cut by widely spaced spiral grooves. Strong corrugation just below the suture. Below the periphery, shell has very fine spiral grooves (more conspicuous than in *Everettia corrugata corrugata*). Height up to 11.3 mm; width up to 18.3 mm; diameter of the first three whorls 1.2–1.4, 0.9–1.1, and 1.6–1.8 mm, respectively; number of whorls up to five; height aperture up to 7.7 mm; width aperture up to 9.8 mm. Genitalia: maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 11.5 mm. The penis, dart-sac, and vagina with thick muscular walls. P, V arranged near the GO then followed by BC and DS where there is little space in the atrium between the openings of P + V and BC + DS. BC about two-thirds of total DS length. Animal: animal head uniform black or grey and extended backward to the end of mantle and downward to the foot-fringe. A grey smear covers large parts of the animal and extends to the end of the tail. The mantle is covered with sparsely distributed bright spots. These bright spots become denser and are agglomerated with the black spots at the last half whorl.

Distribution and habitat: Upper montane primary and coniferous forest, 2800–3500 m alt. Sabah: Mount Kinabalu (only found along the south-eastern slope), endemic (Fig. 9D).

Remarks: Everettia corrugata corrugata and *Everettia corrugata williamsi* occur allopatrically at approximately the same elevational zone (2800–3500 m) but on different ridges which are separated by a deep valley.

EVERETTIA LAYANGLAYANG SP. NOV.

Types: MALAYSIA: State of Sabah: Ranau District. Southern part of Kinabalu Park. At 3112 m alt. along Kotal's route from Bukit Babi to the eastern ridge of Mount Kinabalu (6°3′N, 116°36′E). Collected by T.-S. Liew, J. Lapidin, Safrie, and Jasilin. 24.iv.2005; holotype, BOR/MOL 4439, Figure 6F; MALAYSIA: State of Sabah: Ranau District. Southern part of Kinabalu Park. At 2200 m alt. along Kotal's route from Bukit Babi to the eastern ridge of Mount Kinabalu (6°3′N, 116°36′E). Collected by T.-S. Liew, J. Lapidin, Safrie, and Jasilin. 24.iv.2005; two paratypes, one in BMNH 20080626 and one in SP 13058.

Etymology: This species is named *layanglayang* after the location on Mount Kinabalu where living snails were first found with their unique mantle pigmentation that differs from other *Everettia* species.

Material examined: SABAH – Mount Kinabalu: BOR/MOL 941, southern slope, 3200 m alt., xi.2001; BOR/MOL 950, southern slope, 1400 m alt., vii.2001; BOR/MOL 920, southern slope, 1400 m alt., iii.2000; BOR/MOL 971, southern slope, 1400 m alt., i.2001; BOR/MOL 1379, southern slope, 1400 m alt., vi.2002; BOR/MOL 2699, southern slope, 2460 m alt., xi.2003; BOR/MOL 4246, southern slope, 1500 m alt., iv.2006; BOR/MOL 4429, southern slope, 2300 m alt., xii.2004; BOR/MOL 4430, southern slope, 2308 m alt., xii.2004; BOR/MOL 4431, eastern slope, iv.2005; BOR/MOL 4432, southern slope, 1600 m alt., iii.2005; BOR/MOL 4433,eastern slope, 2300 m alt., iv.2005; BOR/MOL 4435, southern slope, 3221 m alt., i.2005; BOR/MOL 4436, southern slope, 2092 m alt., iv.2005; BOR/MOL 4437, southern slope, 2120 m alt., iv.2005; BOR/MOL 4438, eastern slope, 2412 m alt., iv.2005; BOR/MOL 4441, southern slope, 2188 m alt., iv.2005; BOR/MOL 4442, eastern slope, 2292 m alt., iv.2005; BOR/MOL 4443, southern slope, 2288 m alt., iv.2005; BOR/MOL 4444, southern slope, 2000 m alt., iv.2005; BOR/MOL 4445, eastern slope, iv.2005; BOR/MOL 4446, western slope, 1776 m alt., xi.2005; BOR/MOL 4447, eastern slope, 2060 m alt., iv.2005; BOR/MOL 4448, southern slope, 1784 m alt., ix.2005; BOR/MOL 4449, southern slope, 2212 m alt., iv.2005; BOR/MOL 4450, southern slope, 2096 m alt., ix.2005; BOR/MOL 4451, southern slope, 1616 m alt., iii.2005; BOR/MOL 4452, southern slope, 1700 m alt., ix.2005; BOR/MOL 4453, eastern slope, 1992 m alt., ix.2005; BOR/MOL 4454, southern slope, 1720 m alt., ix.2005; BOR/MOL 4455, southern slope, 2108 m alt., ii.2005; BOR/MOL 4456, eastern slope, 1952 m alt., iv.2005; BOR/MOL 4457, southern slope, iii.2005; BOR/MOL 4458, eastern slope, 2280 m alt., iv.2005; BOR/MOL 4459, southern slope, 2040 m alt., iv.2005; BOR/MOL 4460, southern slope, 2244 m alt., iv.2005; BOR/MOL 4461, eastern slope, 2604 m alt., iv.2005; BOR/MOL 4462, southern slope, 2244 m alt., iv.2005; BOR/MOL 4463, southern slope, 2528 m alt., iv.2005; BOR/MOL 4464, southern slope, 2078 m alt., ii.2005; BOR/MOL 4460, western slope, 1776 m alt., xi.2005; BOR/MOL 4466, southern slope, 1700 m alt., ii.2005; BOR/MOL 4467, southern slope, 1784 m alt., ix.2005; BOR/MOL 4468, southern slope, 2560 m alt., iv.2005; BOR/MOL 4469, southern slope, 2244 m alt., iv.2005; BOR/MOL 4470, southern slope, 1723 m alt., xii.2004; BOR/MOL 4471, southern slope, 2356 m alt., iv.2005; BOR/MOL 4472, southern slope, 2628 m alt., iv.2005; BOR/MOL 4473, eastern slope, 2412 m alt., iv.2005; JJ 1190, southern slope, 1500 m alt., viii, 1986; JJ 13022, southern slope, 2100 m alt., vii.2005; SP 12504, southern slope, 1800 m alt., iv.2005; SP 12924, southern slope, Marai-parai, v.2007; BMNH 20080204, southern slope, 1900 m alt., viii.1967. Crocker Range: BOR/MOL 968, Mount Emas, vii.2000; SP 12907, Mount Alab, 1800 m alt., iii.2007. Mount Trusmadi: BOR/MOL 1384, 1600 m alt., iii.2002; BOR/MOL 1386, 1600 m alt., iii.2002.

Diagnostic characteristics: Uniform pinkish, reddish brown or black animal with unique and regular spot markings on the mantle.

Description: Shell (Figs 6F, 3C, E): large, rather thin, yellowish brown to reddish brown. Spire moderately elevated, outer whorls almost rounded below the suture. Periphery almost rounded. Above the periphery, shell silky with very weak oblique wrinkling, slightly stronger towards the suture. Amongst this wrinkling, very fine granulation (40× magn.), is arranged obliquely. Below the periphery, shell has fine, densely placed spiral grooves. Height up to 10.7 mm; width up to 17.7 mm; diameter of the first three whorls 0.9–1.1, 0.8–1.0, and 1.4–1.6 mm, respectively; number of whorls up to five and one-quarter; height aperture up to 7.4 mm; width aperture up to 9.3 mm. Genitalia (Fig. 7F): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 14 mm. The penis, dart-sac, and vagina with thick muscular walls. P, V arranged near the GO then followed by BC and DS where there is little space in the atrium between the openings of P + V and BC + DS. BC almost same as DS length. Animal (Figs 4E, 8B): the whole animal head is uniformly pinkish, reddish brown, or black. The mantle is darker grey and covered by sparsely distributed tiny brighter spots. These brighter spots become bigger and regularly arranged at the last half whorl.

Distribution and habitat: Primary forests. Sabah: Mount Kinabalu (1800–2600 m) (Fig. 9D).

Remarks: There are only slight differences in shell morphology between *E. subconsul* and *E. layanglayang*; the preceding has regular, dense and moderate corrugation at the suture. However, the body colour and colour pattern of *E. layanglayang* are very different from *E. subconsul*. Some preliminary evidence from animal morphology and the genetic data suggest that hybridization in the contact zone between *E. subconsul* and *E. layanglayang* is occurring: the animal head colour patterns show high consistency within species but the populations in the overlap between the distribution ranges of *E. subconsul* and *E. layanglayang* have an intermediate head colour pattern

(Fig. 4G–I, all from different populations at Crocker Range around 1200 to 1400 m).

EVERETTIA LAPIDINI SP. NOV.

Everettia subconsul, Laidlaw, 1937: 180.

Types: MALAYSIA: State of Sabah: Ranau District. Southern part of Kinabalu Park. At 1900 m alt. Mesilau Resort (6°2′N, 116°35′E). Collected by Martinah, David, and Safrie. Date: 11.v.2007, holotype, SP 12914, Figure 6A; two paratypes, one in BMNH 20080636 and one in BOR/MOL 5500.

Etymology: This species is named after Johny Lapidin, a staff member at Kinabalu Park, who dedicatedly assisted the first author during the intensive malacological survey on Mount Kinabalu in 2005.

Material examined: SABAH – Mount Kinabalu: BOR/MOL 973, southern slope, 1800 m alt., i.2001; BOR/MOL 5320, southern slope, 2244 m alt., iv.2005; BOR/MOL 5321, southern slope, 2040 m alt., iv.2005; BOR/MOL 5265, southern slope, 1950 m alt., ix 2003; SP 12121, southern slope, Kiau view trail, ii.2002; SP12460, southern slope, 1900 m alt., iii.2005; SP 12500, eastern slope, Mansaranam, Kg. Pahu, v.2005; SP12916, southern slope, 1900 m alt., v.2007; SP12924, southern slope, Marai-parai, v.2007; SP 13019, southern slope, 1800 m alt., iii.2008; SP12924, southern slope, Marai-parai, v.2007; BMNH 20080202, southern slope, 1600 m alt., viii.1967; BMNH 20080203, southern slope, 2000 m alt., viii.1967. Mount Trusmadi: BOR/MOL 1293, Waras cave, 1600 m alt., iii.2002.

Diagnostic characteristics: The shell shape of this species is similar to *Everettia klemmantanica*, but the spiral striation above the shell characterizes this species, compared with the granule-like sculpture in *E. klemmantanica*.

Description: Shell (Figs 6A, 11C): large, rather thin, yellowish brown. Spire moderately elevated, outer whorls shouldered below the suture. Periphery slightly shouldered to almost rounded, more distinctly angular in juveniles. Above the periphery, shell shiny with very weak (but distinct) oblique wrinkling, slightly stronger towards the suture and with densely, regularly placed spiral grooves, *c.* 7–8 per mm. Below the periphery, shell has fine, densely placed spiral grooves. Height up to 16.6 mm; width up to 29.0 mm; diameter of the first three whorls 1.4–1.5, 1.0–1.1, and 2.0–2.1 mm, respectively; number of whorls up to five and a half; height aperture up to 12.1 mm; width aperture up to 16.0 mm. Genitalia (Fig. 7B): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 19 mm. The penis, dart-sac, and vagina with thick muscular walls. P, V arranged near the GO then followed by BC and DS where there is much space in the atrium between the openings of P + V and BC + DS. BC about two-thirds of total DS length. Animal (Fig. 8J): the whole animal head is uniformly black. The mantle is black and covered by sparsely distributed tiny bright spots and followed by regularly spaced radial black bands at the last half whorl.

Distribution and habitat: Montane primary forest, from 1400 to 2000 m alt. Sabah: Mount Trusmadi, Mount Kinabalu (Fig. 5C).

Remarks: Spiral striation on the shell is the key character for this species. The animals usually have a uniform black head, but there is a rare case where a white stripe is present between the tentacles, which is similar to the pattern in *E. klemmantanica*. Some immature specimens have only a few spiral striations above the shell near the periphery, and are distinctly shouldered at the periphery. We believe that this species was first collected in 1929 on Mount Kinabalu (1600 m; Pendlebury & Chasen, 1932) and Laidlaw (1937) mentioned that the shells were 'definitely shouldered at the periphery, and like other Kinabalu specimens seem to me to differ from the type of *subconsul* in the British Museum'.

EVERETTIA INTERIOR SP. NOV.

Types: MALAYSIA: State of Sabah, Pensiangan District, Sapulut area. Limestone – Batu Sanaron (4°42′N, 116°36′E). Collected by T.-S. Liew, M. Schilthuizen, and S. Chiba. Date: 25.vi.2005, holotype, BOR/MOL 4277, Figure 2C; ten paratypes, five in BMNH 20080627 and five in SP 13059.

Etymology: This species is named *interior* for its distribution range in the interior of Sabah.

Material examined: SABAH – Sapulut: BOR/MOL 921, Sanaron cave, 450 m alt., vii.2000; BOR/MOL 929, Batu Temurung, ii.2001; BOR/MOL 939, Sanaron cave, vii.2000; BOR/MOL 969, Batu Sinobang, 450 m alt., ii.2001; BOR/MOL 1137, Batu Tinagas, 450 m alt., vii.2000; BOR/MOL 4305, Sanaron cave, vi.2005; BOR/MOL 4332, Batu Punggul, vi.2005; JJ 1304, Pun Batu, ix.1986; JJ 1974, Batu Punggul, v.1987; JJ 5627, Batu Sinobang, 1997; JJ 7546, Batu Pungiton, vii.2000; JJ 7626, Batu Tinagas, vii.2000; JJ 7662, Sanaron cave, vii.2000; JJ 7726, Kg. Labang, vii.2000; JJ 7995, Batu Sinobang, ii.2001; JJ 8038, Batu Temurung, ii.2001; JJ 8069, Sanaron cave, ii.2001.

Diagnostic characteristics: Shell suture depressed with widely placed spiral grooves.

Description: Shell (Figs 2C, 3A): medium-sized, rather thin, brownish, moderately elevated, outer whorls rounded. Periphery rounded, suture depressed. Above the periphery, shell shiny with widely placed spiral grooves, *c.* 4–5 per mm, numerous fine spiral striae in between grooves. Below the periphery, shell has fine, densely placed spiral grooves. Height up to 11.4 mm; width up to 19.7 mm; diameter of the first three whorls 1.0–1.1, 0.9–1.0, and 1.7–1.8 mm, respectively; number of whorls up to five; height aperture up to 8.2 mm; width aperture up to 10.7 mm. Genitalia (Fig. 7H): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 13 mm. The penis, dart-sac, and vagina with thick muscular walls. P, V, GO, BC, and DS arranged around the short genital atrium, limited space between the openings of each of the genital structures. The BC is short, about one-third of total DS length. ANIMAL (Figs 4B, 8E): black bands on either side of the tentacles, which are separated by a white band that occupies the space between the eye tentacles. Black bands extend downward to just below the eye tentacles and backward from the umbilicus region to the end of the tail, downward to the edge of the foot. The mantle is black and covered by crowded tiny brighter spots and followed by regularly spaced radial black bands at the last half whorl.

Distribution and habitat: Primary forest. Sabah: Sapulut area (Fig. 5B).

EVERETTIA PAULBASINTALI SP. NOV.

Types: MALAYSIA. State of Sabah. Tawau District, Tawau Hills Park (04°27′N, 117°55′E). Collected by T.-S. Liew and Johny Lapidin. Date: viii.2007, holotype, BOR/MOL 5498, Figure 6D; four paratypes, two in BMNH 20080628 and two in SP 13060.

Etymology: This species is named after Paul Basintal, director of Sabah Parks, who has served for over 33 years in Sabah Parks.

Material examined: SABAH – Tabin Wildlife Reserve: BOR/MOL 924, Head Quarters, iii.2000; BOR/MOL 926, Base Camp x.2000; BOR/MOL 962, v.2001; BOR/MOL 964, v.2001; BOR/MOL 928, Tabin Limestone, x.2000. Danum Valley: BOR/MOL 5271, v.2000; BOR/MOL 977, v.2000. Imbak Valley: BOR/MOL 927, Transit Camp, vi.2000; BOR/MOL 5264, Transit Camp, vi.2000; SP 12102, vii.2000. Kinabatangan: BOR/MOL 1294, Batu Materis, v.2002; BOR/MOL 2310, Sukau, 2003; BOR/MOL 3597, Gomantong, i.2004; BOR/MOL 5267, Bod Tai, v.2002. Tawau: BOR/MOL 1297, Tawau Hills Park, ii.2002; BOR/MOL 4268, Tawau Hills Park, v.2005; SP 12704, Tawau Hills Park, i.2006; SP 12902, Tawau Hills Park, Mount Magdelena, ii.2007; SP 12193, Tawau Hills Park, ix.2002; SP 12195, Tawau Hills Park, ix.2002; SP 12196, Tawau Hills Park, ix.2002; SP 12226, Tawau Hills Park, iii.2003; JJ 1876, Batu Baturong, i.1987; JJ 7592, Batu Baturong, vii.2000; JJ 13165, Tawau Hills Park, v.2005; JJ 13195, Tawau Hills Park, v.2005; JJ 13208, Tawau Hills Park, v.2005. Lahad Datu: JJ 1255, Segama Valley, Kirk's Cave, ix.1986; JJ 7499, Segama valley, vii.2000; JJ 7789, Segama valley, x.2000.

Diagnostic characteristics: Shell surface with densely placed radial threads.

Description: Shell (Figs 6D, 10D, E): large, rather thin, yellowish brown. Spire moderately elevated, outer whorls slightly shouldered below the suture. Periphery slightly shouldered to almost rounded, more distinctly angular in juveniles. Above the periphery, shell silky with very densely placed radial threads and somewhat cut by irregularly spaced spiral grooves. Below the periphery, shell has fine, densely placed spiral grooves. Height up to 19.5 mm; width up to 25.5 mm; diameter of the first three whorls 0.8–0.9, 0.7–0.8, and 1.4–1.5 mm, respectively; number of whorls up to five and a half; height aperture up to 13 mm; width aperture up to 13.5 mm. Genitalia (Fig. 7C): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 14 mm. The penis, dart-sac, and vagina with thick muscular walls. P, V, GO, BC, and DS arranged around the short genital atrium, limited space between the openings of each of the genital structures. BC about one-quarter to one-third of total DS length. Animal: black bands on either side of the tentacles separated by a white band that occupies the space between the eye tentacles, and extends backward to the end of the mantle and downward to just below the eye tentacles. Other parts of the animal are covered by regularly spaced oblique dotted belts. The mantle is covered by black irregular markings and followed by regularly spaced radial darker brown bands at the last half whorl.

Distribution and habitat: Primary forest until 1400 m. Sabah: Danum Valley, Kinabatangan, Tabin Wildlife Reserve, Tawau Hills Park, Imbak Valley (Fig. 5B).

Remarks: Some of the populations on the left bank of the Segama river (area around Imbak Valley, Danum Valley, and Kinabatangan) have coarser radial

threads and these are cut by more closely placed spiral grooves than in the populations with typical sculpture from the right bank of the Segama river (Tabin and Tawau area).

EVERETTIA JUCUNDIOR SP. NOV.

Everettia subconsul, Laidlaw, 1931: 196–200, figures 3, 4, 6.

Type material: MALAYSIA: State of Sabah: Tawau District. Tawau Hills Park (4°24′N, 117°53′E). Collected by Jacqueline Peter King. Date: xii.2001, holotype, BOR/MOL 1375, Figure 2F; MALAYSIA: State of Sabah: Kinabatangan District. Bod Tai limestone (5°31′N, 118°13′E). Collected by Menno Schilthuizen. Date: 16.v.2002, one paratype in BMNH 20080629.

Etymology: This species is named *jucundior* because of its shell surface sculpture: similar to (but even more jocund than) that of *Everettia jucunda*.

Material examined: SABAH – Tawau: BOR/MOL 922, Batu Baturong 100 m alt., vii.2000; BOR/MOL 1376, Tawau Hills Park, ii.2002. Lahad Datu: JJ 1215, Segama Valley, Kirk's Cave, ix.1986. Tabin Wildlife Reserve: BOR/MOL 5268, i.2005. Danum Valley: BOR/MOL 1231, v.2000. Kinabatangan: BOR/MOL 1387, Batu Tomanggong Besar, iv.2002; BOR/MOL 5269, Batu Mawas, iii.2003; BOR/MOL 5270, Bod Tai, v.2002; BMNH 1897.5.13.2-5, Abai river, 1897; BMNH 1897.5.13.1, Abai river, 1897. Crocker Range: ZMA 176863, Keningau, Kampung Matou, i.1965. Semporna: JJ 1823, Segarong Hills, Batu Tengar, i.1987.

Diagnostic characteristics: Shiny shell with dense spiral striation above shell. The species differs from *E. jucunda* (which has similar sculpture) in terms of the shell shape and size (*E. jucundior* with five whorls and shell 19 mm in width vs. *E. jucunda* – with six and a half whorls and shell 17 mm in width).

Description: Shell (Figs 2F, 11F): medium-sized, rather thin, brownish, moderately elevated, outer whorls slightly shouldered or rounded. Periphery rounded. Above the periphery, shell shiny with densely placed spiral striation, *c.* 20–30 striae per mm. Below the periphery, shell has fine, densely placed spiral grooves. Height up to 10.9 mm; width up to 19.5 mm; diameter of the first three whorls 0.9, 0.8, and 1.3 mm, respectively; number of whorls up to five and one-fifth; height aperture up to 8.3 mm; width aperture up to 10.1 mm. Genitalia (Fig. 7G): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 11 mm. The penis, dart-sac, and vagina with thick muscular walls. P, V, GO, BC, and DS arranged around the short genital atrium, with limited space between the opening of each of the genital structures. BC short, about one-third of total DS length. Animal (Fig. 8H): black bands on either side of the tentacles, which are separated by a white band that occupies the space between the eye tentacles and extends downward to just below the eye tentacles. Grey smear on either side of the tail extending from the umbilicus region to the end of the tail. Other parts of the animal are clear from any markings. The mantle is black and covered by crowded tiny bright spots and followed by regularly spaced radial black bands in the last half whorl.

Distribution and habitat: Primary forest. Sabah: Kinabatangan, Tawau Hills Park, Danum valley (Fig. 5C).

Remarks: The specimens in Laidlaw (1931) were collected by R. Hanitsch in 1899 in British North Borneo. According to the description by Laidlaw, these shells' size and sculpture fit with the material we consider as *E. jucundior*. Some material in the RMNH and JJ collections from Balikpapan (Southeast Coast of Kalimantan) and Sarawak' Fourth Division have similar spiral striation and shell shape but we do not include them in this Sabah *Everettia* revision. Our genetic data also show that *E. jucundior* is not closely related to other Sabah lowland *Everettia* species.

EVERETTIA JASILINI SP. NOV.

Types: MALAYSIA: State of Sabah: Kota Belud District. North-western part of Kinabalu Park. At 2900 m alt. along the trail from Sayap Substation to Nonohan peak (6°7′N, 116°43′E). Collected by T.-S. Liew, J. Lapidin, Dominik, and Jasilin. Date: 25.xi.2005, holotype, BOR/MOL 5318, 12A; four paratypes, two in BMNH 20080630 and two in SP 13062.

Etymology: This species is named after Jasilin, an experienced mountain guide from Kampung Mesilau, who, during the intensive malacological survey on Mount Kinabalu in 2005, made possible many field-trips to remote areas on Mount Kinabalu.

Material examined: SABAH – Mount Kinabalu: BOR/MOL 5311, eastern slope, 3416 m alt., vi.2005; BOR/MOL 5314, eastern slope, 3376 m alt., vi.2005; BOR/MOL 5315, eastern slope, 3320 m alt., vi.2005; BOR/MOL 5317, eastern slope, 3084 m alt., vi.2005; BOR/MOL 5312, western slope, 3008 m alt., xi.2005; BOR/MOL 5313, western slope, 2816 m

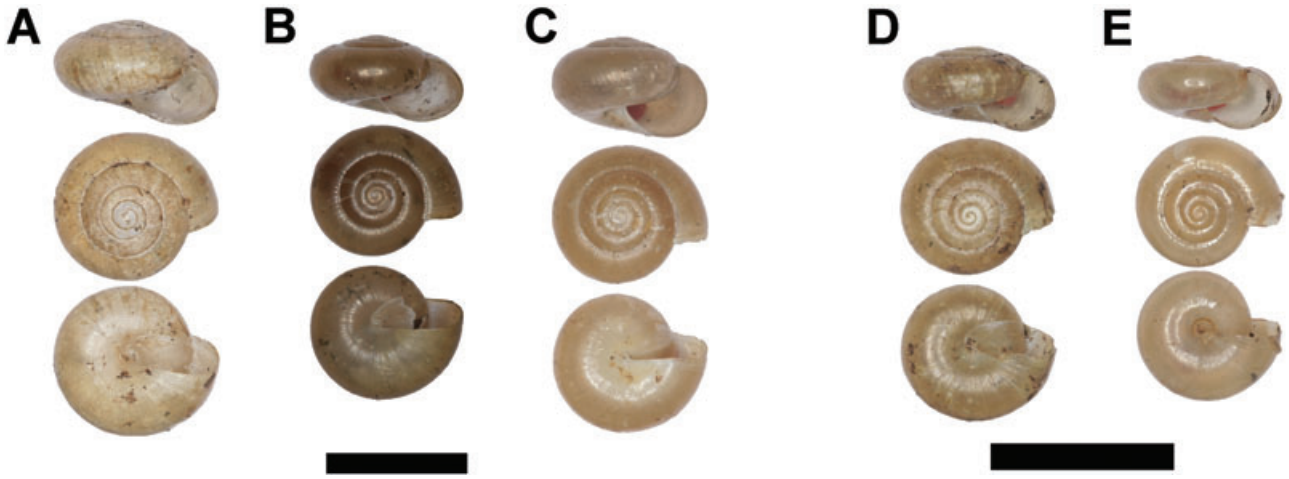

Figure 12. Shells. A, ***Everettia jasilini* sp. nov.**; B, ***Everettia monticola* sp. nov.**; C, ***Everettia dominiki* sp. nov.**; D, ***Everettia safriei* sp. nov.**; E, ***Everettia planispira* sp. nov.** Scale bar = 10 mm.

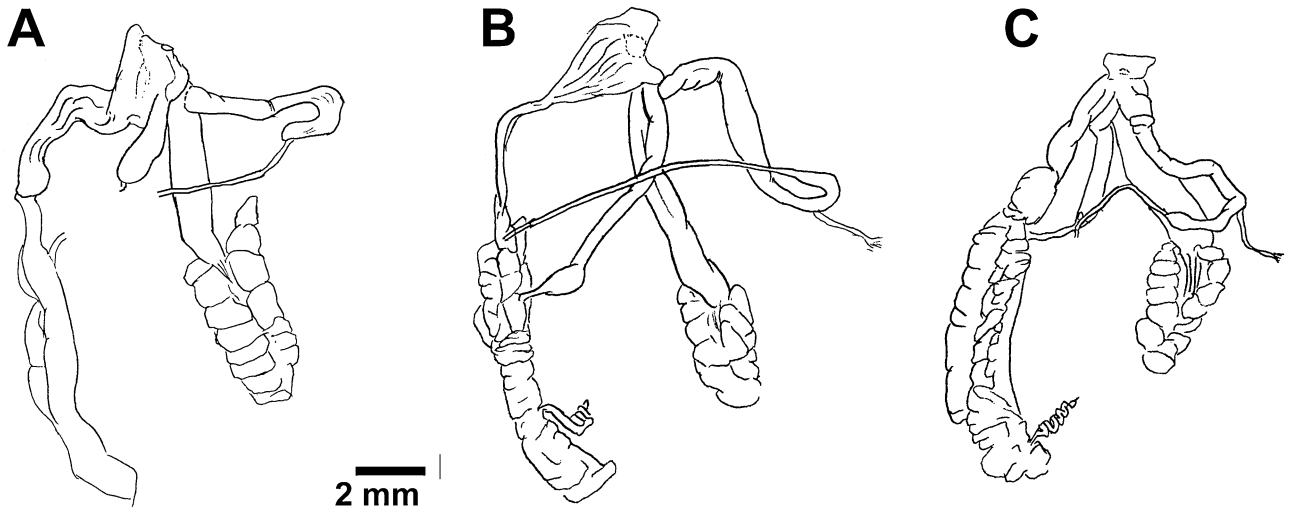

Figure 13. Genitalia. A, ***Everettia jasilini* sp. nov.**; B, ***Everettia dominiki* sp. nov.**; C, ***Everettia safriei* sp. nov.**

alt., xi.2005; BOR/MOL 5316, western slope, 2672 m alt., xi.2005; BOR/MOL 5319, western slope, 2816 m alt., xi.2005.

Diagnostic characteristics: Fine and regularly placed nodules on the upper and lower surface of the shell.

Description: Shell (Figs 10A, B, 12A): small, rather thin, yellowish brown, moderately to distinctly elevated, outer whorls slightly shouldered below the suture. Periphery rounded. Above the periphery, shell silky with distinct oblique wrinkling; fine (40× magn.) but very distinct nodules are arranged spirally (20–35 rows per whorl) on top of the wrinkling. Below the periphery, shell without or with indistinct, widely spaced spiral rows of nodules (2–4 per mm). Height up to 6.8 mm; width up to 10.7 mm; diameter of the first three whorls 0.75–0.8, 0.6–0.65, and 1.0–1.1 mm, respectively; number of whorls up to four and seven-eighths; height aperture up to 4.3 mm; width aperture up to 5.5 mm. Genitalia (Fig. 13A): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 6 mm. The penis and dart-sac have a thin muscular wall and the vagina has a very thin transparent wall. P, V, GO, BC, and DS arranged around the short genital atrium, with limited space between the openings of each of the genital structures. BC short, about half of total DS length. Animal: the whole animal head is uniformly black. The mantle is black and covered by sparsely distributed tiny bright spots.

Distribution and habitat: Upper montane primary and coniferous forest, 3100–3500 m alt. Sabah: Mount Kinabalu, endemic (eastern and northern ridges only; Fig. 9B).

Remarks: Phylogenetic data show that this species is closely related to *Everettia safriei*.

EVERETTIA SAFRIEI SP. NOV.

Types: MALAYSIA: State of Sabah: Ranau District. Southern part of Kinabalu Park. At 2300 m alt. along Kotal's route from Bukit Babi to the eastern ridge of Mount Kinabalu (6°3′N, 116°36′E). Collected by T.-S. Liew, J. Lapidin, Safrie, and Jasilin. 24.iv.2005, holotype, BOR/MOL 5307, Figure 12D; six paratypes, three in BMNH 20080631 and three in SP 13063.

Etymology: This species is named after Safrie Hatimin, staff member at Kinabalu Park, who dedicatedly assisted the first author during the intensive malacological survey on Mount Kinabalu in 2005.

Material examined: SABAH – Mount Kinabalu: BOR/MOL 2671, southern slope, 3330 m alt., x.2003; BOR/MOL 2672, southern slope, 3330 m alt., x.2003; BOR/MOL 2682, southern slope, 3080 m alt., x.2003; BOR/MOL 2683, southern slope, 3080 m alt., x.2003; BOR/MOL 2687, southern slope, 3080 m alt., x.2003; BOR/MOL 5302, southern slope, 3024 m alt., ix.2005; BOR/MOL 5306, southern slope, 3089 m alt., xii.2004; BOR/MOL 5303, eastern slope, 3264 m alt., vi.2005; BOR/MOL 5304, eastern slope, 3352 m alt., vi.2005; BOR/MOL 5305, eastern slope, 3432 m alt., vi.2005; BOR/MOL 5308, eastern slope, 3416 m alt., vi.2005; BOR/MOL 5309, eastern slope, 2924 m alt., iv.2005; BOR/MOL 5310, eastern slope, 3336 m alt., vi.2005.

Diagnostic characteristics: The numerous, irregular, very fine, and discontinuous spiral threads on the upper surface of the shell differentiate this species from individuals of *Everettia dominiki* with similar shell shape and size.

Description: Shell (Figs 10C, 12D): small, rather thin, greenish brown, moderately elevated, outer whorls rounded. Periphery rounded; spire almost flat. Above the periphery, protoconch smooth (sometimes with inconspicuous, densely placed spiral threads); shell with distinct oblique wrinkling; there are very fine, irregular and discontinuous spiral threads above the wrinkling. Below the periphery, shell is almost smooth. Height up to 4.8 mm; width up to 8.3 mm; diameter of the first three whorls 0.75–0.8, 0.55–0.60, and 0.95–1.00 mm, respectively; number of whorls up to five and one-quarter; height aperture up to 3.6 mm; width aperture up to 4.5 mm. Genitalia (Fig. 13C): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 4.5 mm. The penis, dart-sac, and vagina with very thin transparent walls. P, V, GO, BC, and DS arranged around the short genital atrium, with limited space between the openings of each of the genital structures. BC short, about half of total DS length. Animal (Fig. 8D): the head of animal head is uniformly black. The mantle is brownish and in the last half whorl has sparse irregular black and bright markings.

Distribution and habitat: Upper montane primary and coniferous forest, 2700–3500 m alt. Sabah: Mount Kinabalu (eastern and southern ridges only), endemic (Fig. 9A).

Remarks: This species occurs sympatrically with *E. safriei*, to which it is also phylogenetically close. However, both species maintain their distinct and unique shell characteristics.

EVERETTIA OCCIDENTALIS SP. NOV.

Types: MALAYSIA: State of Sabah: Sipitang District. Upper Padas, forest patch near Long Pa Sia village. At 1200 m alt. (4°24′N, 115°44′E). Collected by T.-S. Liew and Meckson. Date: 17.vi.2006, holotype, BOR/MOL 4345, Figure 2E; eight paratypes, four in BMNH 20080632 and four in SP 13064.

Etymology: This species is named *occidentalis* for its distribution range in the western mountain ranges of Sabah.

Material examined: SABAH – Crocker Range: BOR/MOL 946, Lian cave, iv.2000. JJ 1087, Lian cave, vii.1986. Tenom: BOR/MOL 1373, Tenom Rafflesia Garden, 400 m alt., vi.2003; BOR/MOL 4244, 350 m alt., i.2006. Sipitang: BOR/MOL 2993, Muaya waterfall, Lumaku, x.2003.

Diagnostic characteristics: Regularly spaced radial grooves above shell which are different from the radial corrugation of *E. dominiki.*

Description: Shell (Figs 2E, 11D): medium-sized, rather thin, brownish, moderately elevated, outer whorls slightly shouldered below the suture. Periphery round to slightly angular. Above the periphery, shell shiny with rather regularly placed radial grooves, *c.* 2–4 per mm. These radial grooves make the shell seem sculptured with radial ridges under the naked eye. Below the periphery, shell has very

fine, shallow, densely placed spiral grooves. Height up to 11.0 mm; width up to 13.0 mm; diameter of the first three whorls 0.9, 0.5, and 1.2 mm, respectively; number of whorls up to four and three-quarters; height aperture up to 4.9 mm; width aperture up to 6.8 mm. Genitalia: unknown. Animal: unknown.

Distribution and habitat: Primary forest. Sabah: Long Pa Sia, Tenom, and Sipitang, interior of Sabah (Fig. 5A).

EVERETTIA PLANISPIRA SP. NOV.

Types: MALAYSIA: State of Sabah: Beluran district. Ulu Tungud Forest Reserve. East of Solonsong River, 400 m alt. (5°49′N, 117°8′E). Collected by M. Schilthuizen, T.-S. Liew, and A. van Til. Date: 14.viii.2004, holotype, BOR/MOL 3213, Figure 12E; two paratypes, one in BMNH 20080633 and one in SP 13065.

Etymology: Planispira. Latin, means flat whorls.

Material examined: SABAH – Danum Valley: BOR/MOL 1041, vii.2001; BOR/MOL 1132, v.2000; BOR/MOL 1139, v.2000; BOR/MOL 1142, iii.2001; BOR/MOL 1143, ix.2000. Tabin Wildlife Reserve: BOR/MOL 1146, v.2001. Kinabatangan: BOR/MOL 1308, Batu Keruak, iv.2002; BOR/MOL 1309, Batu Keruak, iv.2002; BMNH 1892.70.20.61, Gomantong, 1892. Mount Kinabalu: BOR/MOL 5358, eastern slope, 1952 m alt., iv.2004; BOR/MOL 5358, eastern slope, 2112 m alt., iv.2004.

Diagnostic characteristics: This species is easy to recognize by its small, shiny shell with flat apex and lack of sculpture on the upper and lower surface of the shell.

Description: Shell (Fig. 12E): small, rather thin, brownish, spire flat to slightly elevated, outer whorls flat to slightly rounded. Periphery rounded. Above the periphery, shell shiny with faded growth lines. Below the periphery, shell is smooth and shiny. Height up to 4.7 mm; width up to 8.3 mm; diameter of the first three whorls 0.8, 0.7, and 0.8 mm, respectively; number of whorls up to four and one-quarter; height aperture up to 3.5 mm; width aperture up to 4.8 mm. Genitalia: unknown. Animal: unknown.

Distribution and habitat: Primary forest 50–2000 m, but becoming very rare above 500 m. Sabah: Kinabatangan, Tabin, Danum valley, and Tawau (east coast of Sabah) (Figs 5D, 9B).

Remarks: This species has a shiny shell and is mainly found on the east coast of Sabah.

EVERETTIA MONTICOLA SP. NOV.

Types: MALAYSIA: State of Sabah: Kota Belud District. Southern part of Kinabalu Park. Near 'Villosa Shelter' at 2900 m alt. along the Summit trail of Mount Kinabalu (6°3′N, 116°33′E). Collected by Tachani. Date: x.2003, holotype, BOR/MOL 2691, Figure 12B; three paratypes, two in BMNH 20080634 and one in SP 13066.

Etymology: This species is named *monticola* for its montane distribution.

Material examined: SABAH – Mount Trusmadi: BOR/MOL 1310, 1600 m alt., iii.2002; BOR/MOL 1138, 880 m alt., x.2001. Crocker Range: BOR/MOL 1312, Ulu kimanis, 1200 m alt., vi.2003; BOR/MOL 1313, Mahua, 1000 m alt., iii.2002; BOR/MOL 1131, Mahua, 1000 m alt., v.2001; BOR/MOL 1136, Mahua, 1000 m alt., vii.2001. Kinabatangan: BOR/MOL 1411, Batu Tomanggong kecil, iv.2002. Meliau Range: BOR/MOL 3214, 640 m alt., viii.2004; BOR/MOL 3215, 650 m alt., viii.2004. Mount Kinabalu: BOR/MOL 5361, southern slope, 1552 m alt., ix.2005; BOR/MOL 5364, southern slope, iii.2005; BOR/MOL 5368, southern slope, 2156 m alt., iv.2005; BOR/MOL 5369, southern slope, 1784 m alt., ix.2005; BOR/MOL 5374, southern slope, 1700 m alt., ii.2005; BOR/MOL 5376, southern slope, iii.2005; BOR/MOL 5378, southern slope, 2112 m alt., iv.2005; BOR/MOL 5365, western slope, 1776 m alt., xi.2005; BOR/MOL 5366, western slope, 1152 m alt., xi.2005; BOR/MOL 5370, western slope, 2480 m alt., xi.2005; BOR/MOL 5371, western slope, 1152 m alt., xi.2005; BOR/MOL 5377, western slope, 1496 m alt., xi.2005; BMNH 20080205, southern slope, Mesilau, vi.1967; BMNH 20080206, southern slope, Mesilau, vi.1967; BMNH 20080207, southern slope, Mesilau, vi.1967. Mount Tambuyukon: BOR/MOL 5372, eastern slope, 1144 m alt., ix.2005; BOR/MOL 5373, eastern slope, 1880 m alt., ix.2005; BOR/MOL 5375, eastern slope, 1584 m alt., ix.2005. Mount Nombuyukon: BOR/MOL 5360, north-eastern slope, 1204 m alt., xi.2005; BOR/MOL 5362, north-eastern slope, 1070 m alt., xi.2005; BOR/MOL 5363, north-eastern slope, 1680 m alt., xi.2005; BOR/MOL 5367, north-eastern slope, 1680 m alt., xi.2005; BOR/MOL 5379, north-eastern slope, xi.2005.

Diagnostic characteristics: This species is without distinct characteristics on the shell, except for the moderately elevated spire, in which it differs from other *Everettia* species of similar size.

Description: Shell (Figs 3G, 12B): medium-sized, rather thin, brownish, spire moderately elevated, outer whorls shouldered below suture. Periphery rounded. Above the periphery, smooth but sometimes with irregularly placed oblique wrinkling that is slightly stronger towards the suture. Below the periphery, shell is with or without fine, shallow spiral grooves. Height up to 7.0 mm; width up to 11.9 mm; diameter of the first three whorls 0.7, 0.5, and 1.0 mm, respectively; number of whorls up to five; height aperture up to 5.4 mm; width aperture up to 6.5 mm. Genitalia (Fig. 13B): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 7 mm. The penis and dart-sac have thin muscular walls, and vagina has very thin transparent wall. P, V, GO, BC, and DS arranged around the short genital atrium, with limited space between the openings of each of the genital structures. BC long, almost same length as DS. Animal (Fig. 8C): black bands on either side of the tentacles, which are separated by a white band that occupies the space between the eye tentacles and extends backward to the end of the mantle and downward to the foot fringe, although in some animals, the head around the tentacles is uniformly black but a white band appears near the end of mantle. Other parts of the animal are covered by regularly spaced oblique dotted belts or a grey smear. The mantle is brownish or greyish and in the last half whorl with sparse irregular black and bright markings.

Distribution and habitat: Tropical lowland and montane primary forest 700–2500 m (common between 1000–1500 m). Sabah: Crocker Range, Trusmadi Range, Mount Kinabalu (Fig. 9A).

Remarks: The shell of this species is similar to *E. robusta*, which was described from Borneo (Gude, 1917). However, it is impossible to determine where in Sabah (if at all) the type was collected.

EVERETTIA DOMINIKI SP. NOV.

Types: MALAYSIA: State of Sabah: Kota Marudu District. North-eastern part of Kinabalu Park. At 1600 m alt. along the trail from Serinsim Substation to Mount Nombuyukon No (6°15′N, 116°40′E). Collected by T.-S. Liew. Date: 9.xi.2005, holotype, BOR/MOL 5360, Figure 12C; six paratypes, three in BMNH 20080635 and three in SP 13067.

Etymology: This species is named after Dominik Tinggoh, staff member at Kinabalu Park, who dedicatedly assisted the first author during the intensive malacological survey on Mount Kinabalu in 2005.

Material examined: SABAH – Mount Kinabalu: BOR/MOL 1314, southern slope, 1450 m alt., vi.2002; BOR/MOL 2691, southern slope, 2865 m alt., x.2003; BOR/MOL 2697, southern slope, 2267 m alt., x.2003; BOR/MOL 2698, southern slope, 2460 m alt., x.2003; BOR/MOL 5380, southern slope, 2112 m alt., iv.2005; BOR/MOL 5381, southern slope, 2404 m alt., iv.2005; BOR/MOL 5383, southern slope, 2096 m alt., ix.2005; BOR/MOL 5385, southern slope, 2628 m alt., iv.2005; BOR/MOL 5386, southern slope, 2288 m alt., iv.2005; BOR/MOL 5388, southern slope, 2308 m alt., xii.2004; BOR/MOL 5390, southern slope, 2526 m alt., xii.2004; BOR/MOL 5392, southern slope, 2552 m alt., ix.2005; BOR/MOL 5396, southern slope, iv.2006; BOR/MOL 5399, southern slope, 3154 m alt., i.2005; BOR/MOL 5400, southern slope, 2896 m alt., ix.2005; BOR/MOL 5401, southern slope, 3024 m alt., ix.2005; BOR/MOL 5402, southern slope, 2896 m alt., xii.2004; BOR/MOL 5403, southern slope, 3088 m alt., ix.2005; BOR/MOL 5405, southern slope, 2528 m alt., iv.2005; BOR/MOL 5408, southern slope, 1948 m alt., iv.2005; BOR/MOL 5410, southern slope, 2092 m alt., iv.2005; BOR/MOL 5412, southern slope, 2040 m alt., iv.2005; BOR/MOL 5413, southern slope, 2120 m alt., iv.2005; BOR/MOL 5414, southern slope, 2120 m alt., iv.2005; BOR/MOL 5417, southern slope, 1784 m alt., ix.2005; BOR/MOL 5419, southern slope, 2484 m alt., xii.2004; BOR/MOL 5398, western slope, 2640 m alt., ix.2005; BOR/MOL 5409, western slope, 1968 m alt., ix.2005; BOR/MOL 5422, western slope, 2576 m alt., ix.2005; BOR/MOL 5387, eastern slope, 2812 m alt., iv.2005; BOR/MOL 5389, eastern slope, 2676 m alt., iv.2005; BOR/MOL 5391, eastern slope, 2132 m alt., iv.2005; BOR/MOL 5404, eastern slope, 1992 m alt., iv.2005; BOR/MOL 5411, eastern slope, 1952 m alt., iv.2005; BOR/MOL 5387, eastern slope, 2812 m alt., iv.2005; BOR/MOL 5415, eastern slope, 2300 m alt., iv.2005; BOR/MOL 5416, eastern slope, 3112 m alt., iv.2005; BOR/MOL 5418, eastern slope, 2992 m alt., iv.2005; BOR/MOL 5420, eastern slope, 3064 m alt., iv.2005; BOR/MOL 5421, eastern slope, 2188 m alt., iv.2005; BMNH 20080208, southern slope, Mesilau, vi.1967; BMNH 20080209, southern slope, Mesilau, vi.1967. Mount Tambuyukon: BOR/MOL 5383, eastern slope, 2288 m alt., ix.2005; BOR/MOL 5384, eastern slope, 2080 m alt., ix.2005; BOR/MOL 5395, eastern slope, ix.2005; BOR/MOL 5397, eastern slope, 1584 m alt., ix.2005; BOR/MOL 5406, eastern slope, 1952 m alt., ix.2005; BOR/MOL 5407, eastern slope, 3260 m alt., ix.2005.

Diagnostic characteristics: Shell surface with dense and regularly radial ribs.

Description: Shell (Figs 3F, 12C): medium-sized, rather thin, brownish, spire moderately to highly elevated, outer whorls shouldered below the suture. Periphery rounded. Above the periphery, shell silky with fine, dense, and regular radial corrugation, *c.* 20 wrinkles per mm. Below the periphery, shell has corrugation that extends from above the periphery and dense shallow spiral grooves, but some individuals with only faded spiral grooves on the bottom surface of the shell or entirely without these. Height up to 8.3 mm; width up to 10.1 mm; diameter of the first three whorls 0.7, 0.9, and 1.2 mm, respectively; number of whorls up to four and a half; height aperture up to 4.7 mm; width aperture up to 5.5 mm. Genitalia (Fig. 13B): maximum length from genital opening to the end of dart-sac (before the visible gland tubules) up to 7 mm. The penis and dart-sac have thin muscular walls but vagina has a very thin transparent wall. P, V, GO, BC, and DS arranged around the short genital atrium, with limited space between the opening of each of the genital structures. BC long, almost as long as DS. Animal (Fig. 8C): black bands on either side of the tentacles, which are separated by a white band that occupies the space between the eye tentacles and extends backward to the end of the mantle and downward to the foot fringe. However, in a few rare cases the animal's head is uniformly black. Other parts of the animal are almost entirely black. Some blackish smears and bright markings are irregularly arranged on the brownish mantle. The mantle in the last half whorl is covered by sparse, irregular black and bright markings.

Distribution and habitat: Montane primary forest 1500–3300 m (common). Sabah: Mount Kinabalu (endemic?) (Fig. 9C).

Remarks: The two morphs of this species – with and without spiral grooves on the underside of the shell, occur sympatrically but the one with these spiral grooves can mainly be found between 2000–2500 m. However, genetic data do not support the monophyly of these two morphs.

RESULTS 2: BIOGEOGRAPHICAL PATTERNS AND MOLECULAR PHYLOGENY

Biogeographical patterns

The genus *Everettia* in Sabah consists of many short-range endemics, which are mainly concentrated in the Trusmadi Range and the Crocker Range, and the latter's highest peak – Mount Kinabalu (4095 m). Four species can only be found above 1200 m on both mountain ranges, namely: *E. themis* (Fig. 5B), *E. layanglayang* (Fig. 9D), *E. lapidini* (Fig. 5C), and *E. klemmantanica* (Fig. 5B). In addition, *E. c. corrugata* (Fig. 9B), *E. c. williamsi* (Fig. 9C), *E. jasilini* (Fig. 9B), and *E. safriei* (Fig. 9A) are local endemics of Mount Kinabalu, occurring from 2500 to 3500 m. Besides the short-range montane faunas, there are three wide-range species in the lowland, namely, *E. subconsul* (Fig. 5A), *E. jucundior* (Fig. 5C), and *E. paulbasintali* (Fig. 5B), which can be found from the eastern slopes of the Maitland range and the Witti Ranges towards the east coast of Sabah (Supporting Information Appendix S1). Moreover, *E. subconsul*, which is variable in shell shape and size, also occurs on the west coast, including the western and eastern slopes of the Crocker Range up to 1200 m, and on offshore islands (Fig. 5A). *Everettia interior* can only be found around the Sapulut area in the interior of Sabah, whereas *E. occidentalis* occurs above 1000 m on the eastern slope of Maligan ranges, which is also a political boundary that separates Sarawak and Brunei from Sabah (Supporting Information Appendix S1).

Genetic distance

For *COI*, the average interspecific sequence divergences between *Everettia* species are greater than 11 %, with the exception of the species pairs of *E. layanglayang – E. themis* (9%), *E. layanglayang – E. interior* (8%), *E. themis – E. subconsul* (8%), *E. safriei – E. jasilini* (6%), and *E. corrugata williamsi – E. safriei* (1%) (Table 2). The intraspecific haplotype divergences in *COI* in *Everettia* are within the range of 0–9 % (Table 2). The *16S* molecular divergence patterns between species are similar to those for *COI*, where all the pairwise sequences differences between species are greater than 5%, and exceed the molecular variation within species (0–4%), except *E. safriei – E. jasilini* (2%). The interspecific sequence divergences in *ITS-1* (data not shown) range from 2–10%, whereas intraspecific distances are 0–4%.

Phylogenetic relationships

The alignment contained 52 taxa and a total of 2004 positions (942 for *ITS-1* nrDNA, 558 for *COI* mtDNA, and 504 for *16S* mtDNA). The selected model, nucleotide frequency, and numbers of parsimony informative and variable characters for all data are shown in Supporting Information Appendix S2. The resulting phylogenetic trees from each data matrix are shown in Supporting Information Appendix S4. The results from both MP and BA analyses give similar trees. All of these trees, with the exception of the one based on *COI* (for both full and third codon position excluded datasets) support the monophyly of each species but the topologies for deep divergences vary amongst the

KEY TO THE SPECIES AND SUBSPECIES OF *EVERETTIA* FROM SABAH

1. Shell surface (away from suture) almost smooth, with occasional weak irregular wrinkling and without distinct microsculpture....2
– Shell surface (away from suture) not smooth, with distinct microsculpture....8
2. Animal head uniform in colour or with a grey smear in between eye tentacles....3
– Animal head with clear white band in between eye tentacles....6
3. Shell without corrugation or with radial riblets at the suture....4
– Shell with strong corrugation at the suture....*Everettia corrugata corrugata* Laidlaw
4. Mantle with regularly spaced radial dark bands at the last half whorl....*Everettia themis* (Smith)
– Mantle without regularly spaced radial dark bands at the last half whorl....5
5. Mantle with regularly arranged bright spots at the last half whorl....***Everettia layanglayang* sp. nov.**
– Mantle with sparse irregular black and bright markings at the last half whorl....***Everettia safriei* sp. nov.**
6. Mantle with sparse irregular black and bright markings at the last half whorl....7
– Mantle with regularly spaced radial dark bands at the last half whorl....*Everettia subconsul* (Smith)
7. Shell with flat to slightly elevated spire....***Everettia planispira* sp. nov.**
– Shell with moderately elevated spire....***Everettia monticola* sp. nov.**
8. Shell surface with continuous spiral grooves....9
– Shell surface with granular sculpture or prominent radial riblets....12
9. First five whorls of the shell larger than 20 mm....***Everettia lapidini* sp. nov.**
– First five whorls of the shell smaller than 20 mm....10
10. Shell with no more than ten fine spiral grooves per mm....***Everettia interior* sp. nov.**
– Shell with more than 15 fine striae per mm....11
11. Shell with fewer than 25 fine striae per mm....***Everettia jucundior* sp. nov.**
– Shell with more than 25 fine striae per mm....*Everettia jucunda* (Pfeiffer)
12. Shell surface with granular sculpture....13
– Shell with prominent radial riblets or grooves....15
13. First five whorls of the shell larger than 20 mm....*Everettia klemmantanica* Gude
– First five whorls of the shell smaller than 20 mm....14
14. First four whorls of the shell larger than 10 mm....***Everettia corrugata williamsi* ssp. nov.**
– First four whorls of the shell smaller than 10 mm....***Everettia jasilini* sp. nov.**
15. Shell with radial grooves....***Everettia occidentalis* sp. nov.**
– Shell with prominent radial riblets....16
16. First four whorls of the shell larger than 15 mm....***Everettia paulbasintali* sp. nov.**
– First four whorls of the shell smaller than 15 mm....***Everettia dominiki* sp. nov.**

various phylogenetic reconstructions (Supporting Information Appendix S4). The *COI* dataset does not provide any good resolution even at subspecies level but the *16S* shows better resolved deeper nodes. Nevertheless, all four data matrices of *16S* and *ITS-1* with their truncated data matrices (with only unambiguously aligned regions) generally support the monophyly of morphologically recognized species (Supporting Information Appendix S4). Moreover, in the phylogenetic analysis of the concatenated dataset, several well-supported clades were identified, which correspond to groups of species that share similar morphologies (Fig. 14). Clade A comprises a group of species with sparse, irregular, black and bright markings on the mantle and this clade was further subdivided into two subclades (i.e. clades A1 and A2), which correspond to two different head colour patterns. The well-supported clade B consists of three species that lack prominent shell surface sculpture, and this group could be further subdivided into two clades with characteristic mantle pigmentation, namely radial regularly spaced dark brown bands and bright spots arranged regularly (clades B1 and B3) with clade B1 subsuming a subclade (B2) that consists of two species with different head colour patterns.

CHARACTER EVOLUTION

We used the phylogenetic tree resulting from the concatenated dataset in the evaluation of character evolution. Most of the species with the same type of shell surface sculpture do not form monophyletic groups (Fig. 14). Conversely, the phylogenetically closely related (sub)species pairs (*E. c. corrugata* – *E. c. williamsi*, *E. jasilini* – *E. safriei*, and *E. klemmantanica* – *E. lapidini*) have very different shell surface sculptures (Table 1; Fig. 14). Thus, shell surface sculptures are not phylogenetically informative for the *Everettia* species. Body colour patterns, however, appear to define clades in *Everettia. Everettia corrugata corrugata*, *E. c. williamsi*, *E. jasilini*, and *E. safriei* form a clade that shares the same irregular

Table 2. Genetic sequence divergences (p-distances) from COI (upper-right) and 16S (lower-left)

	planispira, monticola, dominiki	klemmatanica	jucundior	paulbasintali	jasilini	safriei	corrugata corrugata	corrugata williamsi	themis	layanglayang	subconsul	jucunda	interior	lapidini	Quantula striata
planispira, monticola, dominiki		0.14	0.14	0.14	0.12	0.12	0.14	0.12	0.13	0.13	0.14	0.11	0.16	0.14	0.12
klemmatanica	0.10		0.16	0.17	0.16	0.15	0.17	0.16	0.15	0.17	0.17	0.13	0.17	0.16	0.15
jucundior	0.12	0.10		0.16	0.16	0.16	0.16	0.16	0.14	0.16	0.15	0.15	0.16	0.17	0.15
paulbasintali	0.11	0.10	0.11		0.16	0.16	0.15	0.16	0.12	0.12	0.14	0.14	0.13	0.15	0.15
jasilini	0.08	0.08	0.10	0.11		**0.06**	0.14	**0.01**	0.13	0.13	0.15	0.11	0.17	0.17	0.15
safriei	0.08	0.09	0.11	0.10	**0.02**		0.13	**0.06**	0.12	0.14	0.14	0.12	0.15	0.17	0.14
corrugata corrugata	0.10	0.10	0.12	0.10	0.08	0.09		0.14	0.13	0.13	0.15	0.13	0.15	0.17	0.16
corrugata williamsi	0.10	0.11	0.12	0.10	0.08	0.09	**0.00**		0.12	0.13	0.14	0.12	0.17	0.16	0.15
themis	0.12	0.12	0.13	0.09	0.12	0.12	0.13	0.12		**0.09**	**0.08**	0.11	0.11	0.15	0.13
layanglayang	0.13	0.13	0.14	0.11	0.11	0.12	0.13	0.13	0.06		0.11	0.13	**0.08**	0.16	0.15
subconsul	0.13	0.12	0.13	0.10	0.12	0.12	0.12	0.12	0.05	0.07		0.14	0.12	0.16	0.15
jucunda	0.13	0.12	0.11	0.12	0.11	0.11	0.14	0.14	0.12	0.14	0.13		0.15	0.14	0.13
interior	0.12	0.09	0.12	0.09	0.10	0.11	0.12	0.12	0.09	0.10	0.09	0.13		0.16	0.17
lapidini	0.10	0.06	0.11	0.12	0.09	0.10	0.12	0.12	0.12	0.13	0.12	0.12	0.10		0.14
Quantula striata	0.21	0.22	0.21	0.22	0.20	0.21	0.21	0.20	0.22	0.23	0.23	0.20	0.23	0.22	

Bold text indicates that the genetic sequence divergence for the species pair is less than 0.10.

black and bright markings on the mantle and a uniform animal head colour (clade A2, Fig. 14). All the large (shell width > 16 mm) lowland *Everettia* species share the same type of head colour pattern and mantle pigmentation despite the fact that many of them are not genetically closely related. Almost all *Everettia* species have a unique combination of characters, from the three character groups (shell surface sculpture, head colour pattern, and mantle pigmentation, see dichotomous key). The three unrelated species *E. jucunda*, *E. interior*, and *E. jucundior*, however, form an exception: they are very similar in the above-mentioned three characters (Table 1).

DISCUSSION

In this revision, the number of known *Everettia* species in Sabah has been increased from five to 17, of which 11 are new species (*E. layanglayang* sp. nov., *E. lapidini* sp. nov., *E. paulbasintali* sp. nov., *E. occidentalis* sp. nov., *E. jasilini* sp. nov., *E. safriei* sp. nov., *E. interior* sp. nov., *E. jucundior* sp. nov., *E. planispira* sp. nov., *E. monticola* sp. nov., *E. dominiki* sp. nov.) and one new subspecies, namely, *E. corrugata williamsi* ssp. nov.). Our revision also confirmed the species status for two taxa that previously had been described on the basis of shell characters only (i.e. *E. subconsul* and *E. klemmantanica*). Furthermore, we found that *Xesta themis* belongs to the genus *Everettia*, as supported by conchological and genetic data. Finally, we have rediscovered two *Everettia* species that had been collected only once since their original description in 1885 (*E. themis sensu* Smith, 1895) and before 1904 (*E. klemmantanica sensu* Gude, 1918), and supplemented data on their distribution and soft part morphology.

On top of the *Everettia* species that are treated in this study, and at least ten more *Everettia* species that have been described from other parts of Borneo, it may be expected that dozens of species still remain to be discovered in the island, as Sabah represents only about ten per cent of the total area. The remarkable number of new species of this genus on a regional scale reflects the incompleteness of our knowledge of the pulmonate snails of tropical Asia.

Our results show that certain aspects of classical morphology-based taxonomy are valid in recognizing *Everettia* species, especially with regard to the shell surface sculpture (see dichotomous key). The unambiguous types of shell surface sculpture show intraspecific consistency, whereas shell size, colour, and shape show great geographical variability, especially in widespread species (e.g. *E. subconsul* and *E. paulbasintali*). However, shell surface sculptures are not phylogenetically informative for the *Everettia* species. The shell surface sculpture apparently

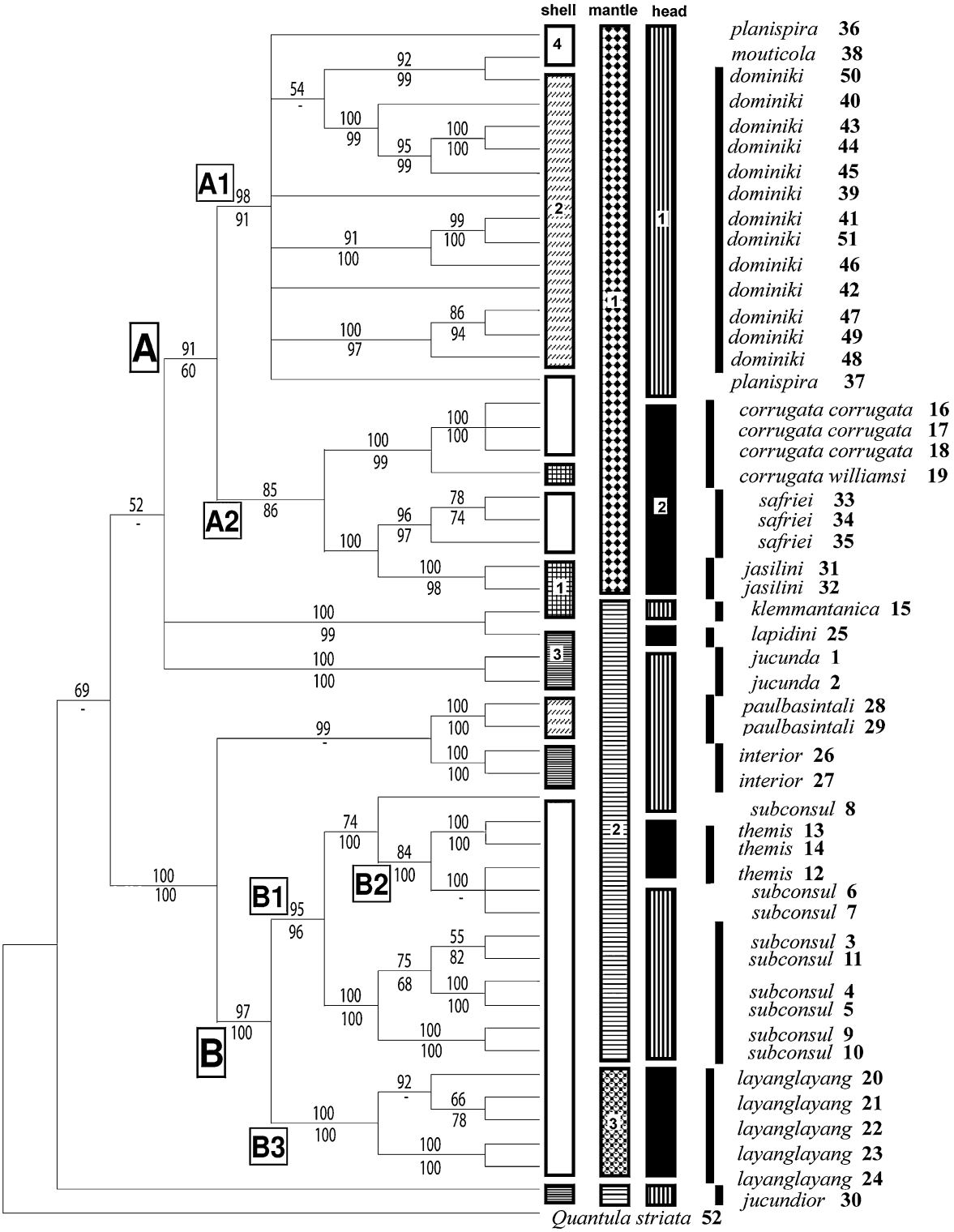

Figure 14. Phylogenetic reconstructions and character evolution. Values at the upper node are bootstrap values from maximum parsimony (MP) and Bayesian analysis (BA) posterior probabilities are at the lower nodes. Both MP and BA support clade A, which consists of species with the same mantle pigmentation, and two subclades, i.e. A1 and A2, characterized by two different head colour patterns. All the species in clade B are without prominent sculpture, but there are discrepancies in mantle and head colour patterns (subclades B1, B2, and B3). For acronyms of the character states and species numbers see Table 1.

evolves rapidly and in parallel or convergently in response to environmental conditions or predation (e.g., Vermeij, 1973; Pfenninger & Magnin, 2001; Schilthuizen *et al*., 2006). Body colour patterns, however (normally not considered a phylogenetically informative suite of characters; Cowie & Jones, 1985; Pinceel *et al*., 2004), appeared to define clades (Fig. 14). For the species that are indistinguishable on the basis of the shell (*E. layanglayang* and *E. subconsul*), the external colour patterns of the soft parts (i.e. mantle pigmentation and head colour patterns) provide resolution for these species (clades B1 and B2, Fig. 14). Richling (2004) remarked on the relationship between mantle pigmentation and shell thickness. She suggested that helicinids with rather thick shells tend to have uniform mantle pigmentation, but that the mantle is mottled in thin-shelled species. Although we did not measure the shell thickness of *Everettia* species in this study, we have the impression that shell thickness does not differ much amongst *Everettia* species. Our observations in the field indicated that mantle mottling was visible through the shell in all species. This, and the fact that mantle pigmentation within species showed little variability and displayed consistent differences amongst species, suggests that colour patterns in *Everettia* may be quite reliable taxonomic indicators. We also noticed that the mantle pigmentation of *E. layanglayang* from two different populations is identical, whereas shell colour varies. In contrast to the situation in helicinids (Richling, 2004), we think that mantle pigmentation of *Everettia* does not show environmental plasticity and has adequate value in systematics. However, because empty shells are encountered more frequently than living specimens in the field, the use of soft part pigmentation for identification purposes is limited. We suggest that identification can best be achieved on the basis of shell characters combined with known distribution ranges.

We found only a limited degree of species differences in the genitalia. Closely related taxon pairs (e.g. *E. lapidini* and *E. klemmantanica*; *E. corrugata corrugata* and *E. c. williamsi*) have almost identical genitalia. Generally speaking, the lowland wide-ranging species have a shorter bursa copulatrix (BC) in proportion to the dart-sac (DS) than the highland species. There are some distinct and unique characteristics in the genitalia of the smaller *Everettia* species (*E. jasilini*, *E. dominiki*, *E. planispira*, *E. monticola*, and *E. safriei*). The first two, for example, have a wide vagina, and *E. safriei* has a very thin penis muscular wall.

Generally, the phylogeny based on mitochondrial and nuclear DNA supports the monophyly (with bootstrap values > 95%) of the species classified on the basis of conchological characters, with the exception of a group of taxa in clade A1 (i.e. *E. dominiki*, *E. planispira*, and *E. monticola*) and *E. themis*, which appears to be polyphyletic within the clade of *E. subconsul* (clade B2). The genetic data do not support the monophyly for each of three *Everettia* species (*E. dominiki*, *E. planispira*, and *E. monticola*) that were classified on morphological grounds (clade A1, Fig. 14). Nevertheless, these three species occur allopatrically (Fig. 9A–C) and *E. dominiki* has a prominent shell surface sculpture that is clearly different from the other two species. We suggest that the poor resolution in clade A1 might be a result of the inadequate representation of *E. planispira* and *E. monticola* in our genetic analysis.

As mentioned in the species descriptions, *E. themis* occurs at an altitudinal zone in between *E. subconsul* and *E. layanglayang* (*c*. 1200–1800 m) and has the same head colour as *E. layanglayang*. It also has mantle pigmentation elements of both *E. layanglayang* and *E. subconsul* (radial bands and bright, regularly placed spots). Moreover, the sequence divergences (i.e. *COI* and *ITS-1*) amongst *E. themis* – *E. layanglayang* – *E. subconsul* are lower than the genetic divergences amongst other species (Table 2). We have yet to elucidate whether this may mean that *E. themis* is a primary or secondary product of hybridization between both highland and lowland parent species.

We also found an interesting phylogeographical pattern of the *Everettia* species on Mount Kinabalu. Four Mount Kinabalu endemic species, namely, *E. corrugata corrugata*, *E. corrugata williamsi*, *E. jasilini*, and *E. safriei*, which occur sympatrically at 2500 –3500 m elevation form a monophyletic group, despite their different shell surface sculptures (Fig. 14). They do, however, have the same mantle pigmentation and animal head colour patterns, which are probably synapomorphies. The sympatric clustering of these closely related endemic species in a small geographical area is unusual as sister taxa are mostly distributed allopatrically and, conversely, sympatric species are normally not closely related. For example, *E. themis*, *E. layanglayang*, and *E. subconsul* are a monophyletic group with no distinct characters on the shell but they are distributed allopatrically at different elevations, where *E. subconsul* reaches from sea-level to *c*. 1200 m, *E. themis* occurs between *c*. 1200–1800 m, and *E. layanglayang* occurs above 1800 m. Furthermore, groups of species that share a certain type of shell sculpture are not monophyletic in the molecular phylogeny (e.g. *E. jucunda*, *E. interior*, and *E. jucundior*, all with spiral striation) and have disjunct distribution patterns (Figs 5A–C, 14). Based on the distribution data, it can be stated that both higher (> 1000 m, e.g. Crocker Range and Trusmadi Range) and lower (< 1000 m, e.g. Maitland Range and

Witti Range) continuous mountain chains in Sabah represent barriers for the distribution of species. However, major rivers do not seem to have a major influence on *Everettia* species distribution.

CONCLUSION

Our results demonstrate that a critical revision of a group of large-shelled, conchologically simple tropical pulmonates may reveal great phylogenetic and cryptic morphological diversity. In this study, we resolved the taxonomic puzzle of the genus *Everettia* in Sabah. *Everettia* species show interestingly disjunct and sympatric distribution patterns, which possibly result from complex orogeny in the area. Furthermore, there are quite a number of highland endemics and possible hybrid zones between species. Therefore, this revision opens the way to studies of the evolution and biogeography of this genus at a regional scale.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Left – map of Sabah and right – map of Kinabalu Park (enlargement of A in map on left), with major geographical features (elevation, rivers and mountain ranges with names) and sampling localities for all the *Everettia* species. Numbers on the map correspond to the specimens collected for genetic analysis (Table 1).
Appendix S2. Parameters for maximum parsimony analysis and Bayesian analysis.
Appendix S3. Types of *Everettia* species deposited in BMNH.
Appendix S4. Phylogenetic trees from six different datasets (see Supporting Information Appendix S3). All datasets were analysed by maximum parsimony (MP) and Bayesian analysis (BA); and bootstrap values of MP and posterior probabilities of BA are indicated above and below the nodes, respectively. A, cladogram from *ITS* full dataset. B, cladogram from *ITS* truncated dataset. C, cladogram from *COI* full dataset. D, cladogram from *COI* truncated dataset. E, cladogram from *16S* full dataset. F, cladogram from *16S* truncated dataset. For acronyms of the species number see Table 1.