

**A new subspecies of *Amphidromus (Goniodromus) bulowi* Fruhstorfer, 1905
(Gastropoda: Pulmonata: Camaenidae) from Sumatra, Indonesia**

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ABSTRACT Since its discovery, the rare arboreal land snail *Amphidromus (Goniodromus) bulowi* Fruhstorfer, 1905 has only been found on the forested slopes of Mount Singgalang, West Sumatra. In 2013, a survey of the forests in western Malalak District of West Sumatra located a new population on Bukit Pandan, which is described herein as *Amphidromus (Goniodromus) bulowi malalakensis* new subspecies. The new subspecies has a dextral whitish shell with a pale grey and/or light buff to tawny open-tent pattern instead of brown, and lacks the creamy, purplish- or pinkish-brown undertones of the amphidromine nominotypical subspecies.

KEY WORDS Malalak District, Agam Regency, *Amphidromus*, *Goniodromus*, *bulowi*, *malalakensis*, new subspecies.

INTRODUCTION

Late 2008, John Abbas was made aware of *Amphidromus (Goniodromus) bulowi* Fruhstorfer, 1905 by Jamie Powers of Edgewater, Florida. This resulted in a trip to the foothills of Mt. Singgalang, West Sumatra to locate this species, 200 m above the type locality of Pandai Sikek. Unfortunately, Pandai Sikek is now a sizable village with much of the low altitude forest transformed for agriculture by the villagers, which has removed the forest mentioned by Rolle (1908) at 4000 to 5000 ft. (1219 to 1524 m) altitude. Sugarcane is the main crop grown and the fields stretch a few hundred metres up from the base of Mt. Singgalang. Even after employing a few villagers, only one specimen was located on the first visit to the area.

Various factors contribute to the difficulty in locating *A. (G.) bulowi* on Mt. Singgalang. Birds prey on snails on the trees and any fallen snails may be eaten by pigs and rodents foraging below. The main factor is shrinking habitat due to agricultural deforestation and forest fires set intentionally by villagers to assist in clearing and for fertilizer. Logging for wood, whether used for housing, furniture or paper, further deforests this mountain. After a few more trips to Mt. Singgalang each year until October 2013 only a limited number of specimens were found, so John chose to explore other areas adjacent to and beyond Mt. Singgalang.

In November 2013, John visited the outer slopes in the south-eastern part of the Lake Maninjau caldera. A colony of snails identified as pale coloured *A. (G.) bulowi* was located on Bukit

Pandan, western Malalak District, some 15 kilometres west of Pandai Sikek. Both Fruhstorfer (1905) and Rolle (1908) never mentioned anything about Malalak. The road dividing west and east Malalak is now sealed, making the area more accessible. A more recent trip by Steven Lie to western Malalak to locate

more specimens of these snails came up empty as local farmers had cleared more forest using the slash-and-burn technique. The Bukit Pandan snails are distinguishable from the nominotypical subspecies by shell coloration, and described herein as *A. (G.) bulowi malalakensis* new subspecies.

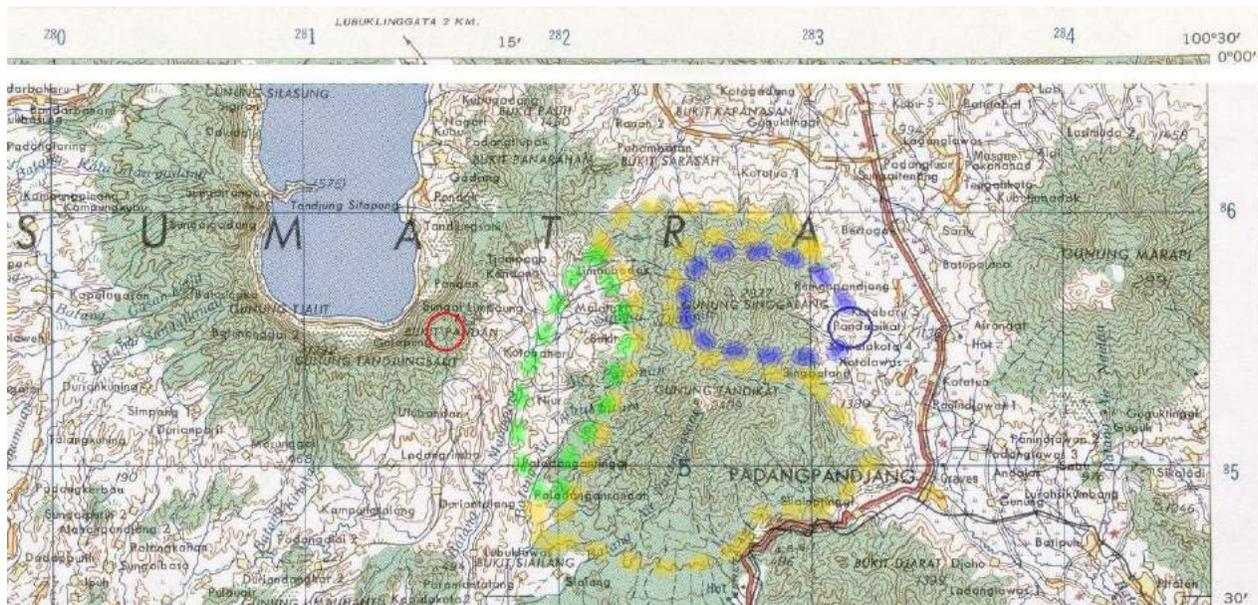


Figure 1. Location map for both subspecies: *A. (G.) bulowi malalakensis* n. ssp. (red circle = type locality), *A. (G.) b. bulowi* (blue circle = type locality, blue dotted line = known range and yellow dotted line = predicted range) and predicted extent of a previous contact zone (green dotted line). Modified from a 1954 map of “Pandang, Sumatra” [contour interval 100 m with supplementary contours at 50 m intervals] (University of Texas Libraries, 2014).

METHODS AND MATERIALS

Type material has been deposited in the Natural History Museum, London, England, UK and Muséum National d'Histoire Naturelle, Paris, France; and three paratypes belong to the private collections of the authors, Jeff Parsons (1 shell) and John Abbas (2 shells). The subspecies description was determined from shell morphology of dry empty shells obtained by John Abbas. Comparative material comprised of shells from the private collections of the authors, and images of type shells from the literature. Photography credits are as indicated below each image. Relative shell sizes

for the subgenus *Goniodromus* Bülow, 1905 mentioned are as follows: small < 35 mm, medium 35–55 mm and large > 55 mm.

Shell sculpture was examined under low magnification (10x) using a jeweller's loupe. Most shells examined had formed a thickened adult lip, and only one had a thin subadult lip. All shells were measured for shell height and shell width including the reflected lip, using digital vernier callipers with a resolution of 0.01 mm. Whorl count includes the apex as per Haniel (1921, p. 22, fig. 10) and counted precise to 0.125 (1/8 whorl). The ratios of shell height to shell width (H/D) were calculated as indices of

shell shape. Shell weight was measured in grams (g) using a pocket-sized electronic scale (capacity 300 g x 0.01 g). Measurement of the perch angle (PA) follows Dharma (2007). The term ‘paries’ (adj. parietal) refers to the ‘inner apertural wall’, and ‘palatum’ (adj. palatal) refers to the interior surface of the ‘outer apertural wall’.

Taxonomic and other remarks

Bülow (1905) established *Goniodromus* as a new subgenus of *Amphidromus* Albers, 1850 on page 83 prior to Fruhstorfer’s paper in the same journal issue. Fruhstorfer (1905) by default selected and named the type species after Bülow as *Amphidromus (Goniodromus) Bülowi*. Laidlaw and Solem (1961) incorrectly stated on page 606 that Fruhstorfer established this species as *Amphidromus bülowi*, i.e. without using *Goniodromus* as the subgenus, and they also use this spelling with the diacritic on pages 587 and 589. The current International Commission on Zoological Nomenclature code (ICZN, 1999) does not allow the use of diacritics in a species name (Articles 11.2 and 27) and such names must be corrected (Article 32.5.2), therefore the accepted spelling is *A. (G.) bulowi*.

Please note that the spellings of the locality names used by Rolle (1908) are correct for the Dutch era, and since independence, the Indonesian government has changed them. Padang Sikeh is now Pandai Sikek and Vulkans Singalang is now Gunung Singgalang.

Abbreviations used for museums and private collections:

CNHM = Chicago Natural History Museum
NHMUK = Natural History Museum, London, England, UK
MNHN = Muséum national d’Histoire naturelle, Paris, France

JA = John Abbas collection

JP = Jeff Parsons collection

Abbreviations for shell morphometry:

D = shell width (the abbreviation aligns with the usage of ‘diameter’ in the literature)

H = shell height

H/D = shell height/shell width ratio

N = whorl count

PA = perch angle

W = shell weight

SYSTEMATICS

Class Gastropoda Cuvier, 1795

Family Camaenidae Pilsbry, 1895

Genus *Amphidromus* Albers, 1850

Subgenus *Goniodromus* Bülow, 1905

Type = *A. (G.) bulowi bulowi* Fruhstorfer, 1905

Amphidromus (Goniodromus) bulowi malalakensis new subspecies

Figs. 2, 3, 4 top and 6C

Type Material: 5 adult shells, all dextral; Holotype (Figure 2): NHMUK 20140066, H 52.10 mm, D 26.10 mm, H/D 2.00, N 7.00 and PA 20.13°; Paratypes (4 shells): Paratype 1 (Figure 3A) MNHN IM-2012-2717, H 52.00 mm (protoconch missing), D 26.10 mm, H/D no data, N 6.00 (calculated) and PA 23.10°; Paratype 2 JP (Figures 3B & 6C) H 53.50 mm, D 26.11 mm, H/D 2.05, N 6.625, W 4.01 g and PA 19.10°; Paratype 3 JA (Figure 3C), H 52.65 mm, D 26.50 mm, H/D 1.99 and PA 24.58°; Paratype 4 JA (Figures 3D & 4 top snail), H 48.47 mm, D 24.10 mm, H/D 2.01 and PA 20.58°.

Other material examined: 4 adult shells, all dextral (Figures 3E-H); H 50.87–51.86 (av. 51.43) mm, D 26.20–27.00 (av. 26.58) mm, H/D 1.92–1.95 (av. 1.94) and PA 19.42–26.66° (av. 21.87°).

Type Locality: Bukit Pandan western Malalak District, Agam Regency, West Sumatra, Indonesia at an altitude of 1389 metres. (Figure 1)

Distribution: currently known only from the type locality; possibly found on other peaks with the same vegetation on the rim of the Maninjau Caldera.

Habitat: found about three metres above the ground on the trunks of trees in a bushy form of submontane forest with *Pandanus*, ferns and herbs.

Animal: mid-body and often the neck are flesh-pink; head, foot and sometimes neck flesh-pink sprinkled with yellowish-orange or reddish-orange granules; mid-dorsal stripe dark grey and narrow to wide, sometimes faint, continuing onto the face; optic and sensory tentacles yellowish-orange; tail flesh-pink with yellowish-orange or reddish-orange margins and tip; mantle and sole not seen.

Etymology: named after the Malalak District where this new subspecies was discovered.



Figure 2. *Amphidromas (G.) bulowi malalakensis* n. ssp., holotype NHMUK 20150226 (Photos by John Abbas).

Description (holotype)

Shell imperforate, medium, dextral, robust and subfusiform-conic with a moderately long spire. Surface shiny; early whorls worn smooth; lower teleoconch microsculpture of crowded spiral microstriae crossed by fine growth lines; and a macrosculpture of growth threads becoming

coarser and more numerous on the last, and overlaid with random or pattern forming malleations. Whorls steadily decrease in convexity and almost flat above the periphery on the last 1.5 whorls. Last whorl not descending in front; its base tapered and compressed obliquely into a strongly protuberant keel, margined by a cord above.

Suture scarcely impressed and periostracum straw-yellow, very faint.

Protoconch of 1.5 whorls, chalk-white and obtuse-conical, demarcated by a stria and ridgelet; apex slightly protruding. Teleoconch translucent greyish-white grading to chalk-white on the last; and an obsolescent white infrasutural fillet on the early whorls. Lower whorls marked with a tawny reticulate pattern

and several opaque grey resting lines, representing former lips; circumcolumellar band white.

Aperture subvertical, subelliptical; base canaliculated and effuse. Palatum gleamy white, translucent and weakly shows the external pattern. Parietal callus colourless, thinly glazed over a buff-yellow paries. A parieto-labral tubercle joins the posterior outer lip

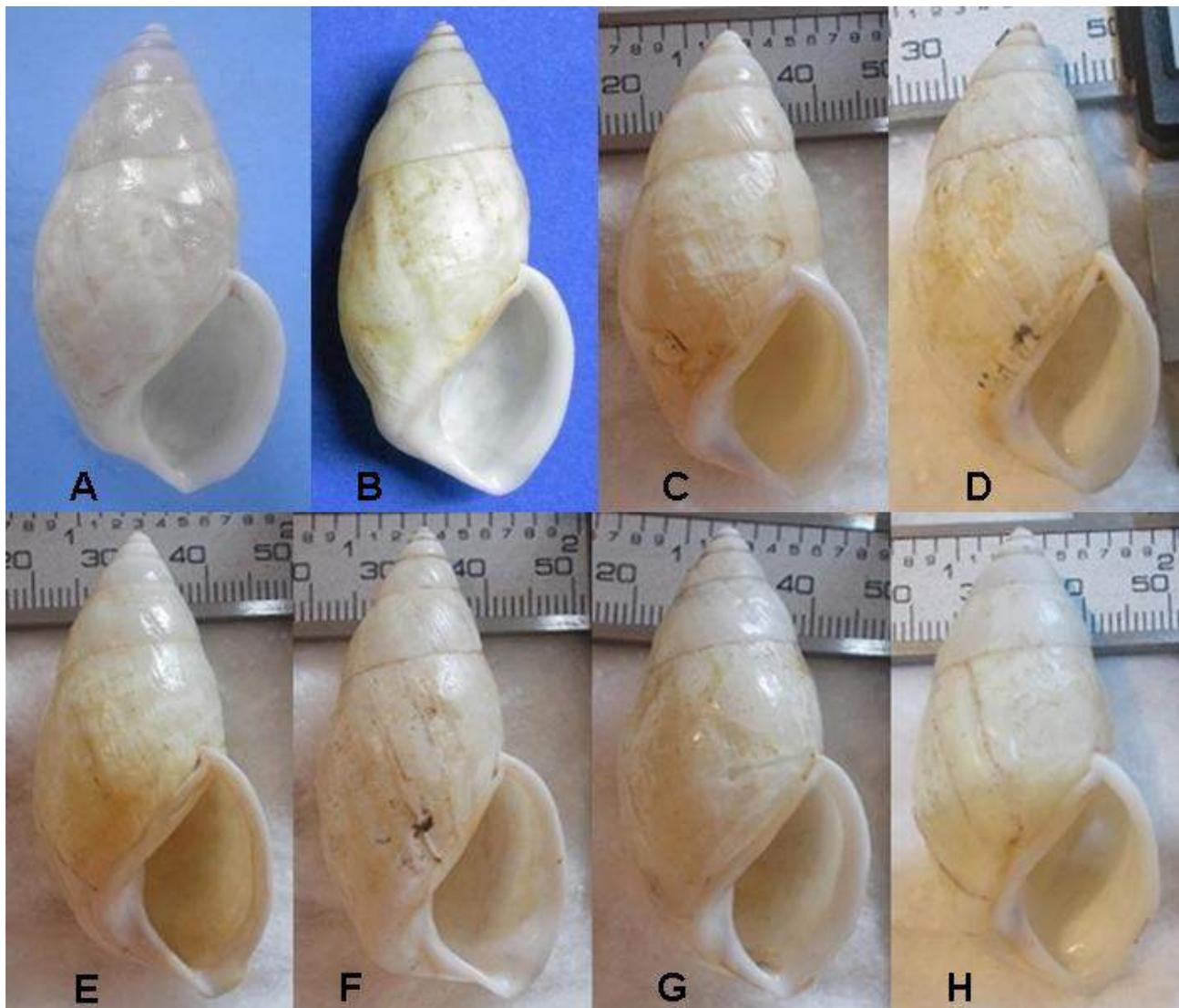


Figure 3. Variation of *A. (G.) b. malalakensis* n. ssp. with the 4 paratypes in the top row: **A** paratype 1, **B** paratype 2, **C** paratype 3 and **D** paratype 4. **E, F, G,** and **H** other material examined. (Photos by John Abbas).

termination; cord of white callus, elongate and extends internally for 3 to 5 mm, faintly grooved along its posterior edge. Outer lip white, broadly reflexed and face rounded; anteriorly flared and flattened toward a shallow notch below, forming a spout (rostrum); edge not recurved and posterior termination slightly ascending. Columella thickened and narrow, upper part vertical; base bent adaperturally, forming a basal lip. Columellar margin callused, forming an adherent shield over part of the keel (columellar callus); outer edge thickened. Umbilicus sealed.

Shell Variation

Subspecies is currently known only from dextral shells with a white ground and grey and/or yellowish-brown markings (Figure 3). Hue intensity of the paries varies from buff-yellow (Figure 6B) to cinnamon-buff. Of 9 shells none are patternless and one has a light buff super medial band on the early teleoconch whorls (Figure 3C). Pattern varies: primary markings are pale grey and/or light buff to tawny irregular, zigzag and/or branching lines and streaks, sometimes interrupted but regularly anastomosing, demarcating “tents” of ground colour and occasionally bordered with white lines. Sometimes random fleshy-ochre or tan longitudinal streaks occur as secondary markings. Ground colour does not vary between shells, although lighting and viewing angle may suggest a yellowish tint ventrally (Figures 3C-D). Live snails tend to have a whitish coating on the periostracum that is lost when cleaned (Figure 4 top snail).

Rostrum varies in extension and depth depending on the angle and protrusion of the keel. The bent base of the columella is longer than the top part in all specimens. Often the margin of the parietal callus is thickened,

connecting it to the thickened margin of columellar callus. The columella's root is weakly grooved or not. No juveniles were found to demonstrate if an umbilicus is present or not. Aperture is narrow to moderately wide and oblong, subtrapezoid (Figure 6C) or subelliptical (Figure 2) at a ratio of 3:4:2. Back of the outer lip is white as per its face. Shell shape varies with angulation of the basal keel. The parieto-labral tubercle is long in all shells and in mature specimens elongates along the parietal callus margin to form an “L” shaped lump when viewed from above.



Figure 4. Live *A. (G.) b. malalakensis* n. ssp. (paratype 4, top snail) compared with *A. (G.) b. bulowi* from Mt. Singgalang (bottom snail) (Photo by John Abbas).

Comparison Material Examined:

A. (G.) bulowi bulowi
Nominotypical subspecies
Figs. 4 bottom, 5, 6A, 6B, 6D and 7

Type material: figured images of 2 out of 4 shells from the type series; H 55–60 mm (Fruhstorfer, 1905); **Lectotype:** sinistral, NHMUK 1910.12.30.98 (Figure 5A); H 54.50 mm, W 27.90 mm, H/D 1.95, N 6.125 and PA

18.42°; Paralectotypes: 2 sinistral (unfigured) and 1 dextral (Figure 5B).

Type Locality: determined by Rolle (1908) as forest at 4000 to 5000 ft. (1219 to 1524 m) altitude on Mt. Singgalang near Pandai Sikek, Sepuluh Koto District, Tanah Datar Regency, West Sumatra, Indonesia; colony extinct due to agricultural deforestation.

Other material examined: photos of 10 live adults (Figure 4 bottom snail); and 15 adult shells (JA, all dextral; Figures 5D, 6A, 6B, 6D & 7); 1 subadult shell (JP, dextral, protoconch missing; fig. 6A) — H 45.73 mm, D 24.63 mm, H/D 1.86, N 5.75, W 1.94 g and PA 23.10°; 1 adult (JP, dextral; Figure 6B) — H 51.31 mm, D 25.74 mm, H/D 1.99, N 6.50, W 4.90 g and PA 21.65°; and 1 shell claimed to be a “paratype” by Laidlaw and Solem (1961), CNHM 72436 (sinistral; Figure 5C).

Locality: broadleaf forest on Mt. Singgalang above Pandai Sikek.

Distribution: eastern flank of Mt. Singgalang above 1500 m altitude; probably found on other parts of Mt. Singgalang, and also on Mt. Tandikat at the same altitude since both volcanoes are connected (twin volcano), but not confirmed. (Figure 1)

Habitat: found on trunks, limbs and branches of tall trees in various types of forest.

Animal: mid-body and neck flesh-pink sprinkled with yellowish-orange granules more concentrated on the head, foot and tail; mid-dorsal stripe narrow to wide, pale to dark grey or black, continuing onto the face; optic tentacles yellowish-orange and sensory tentacles paler; mantle collar flesh pink and sole not seen.

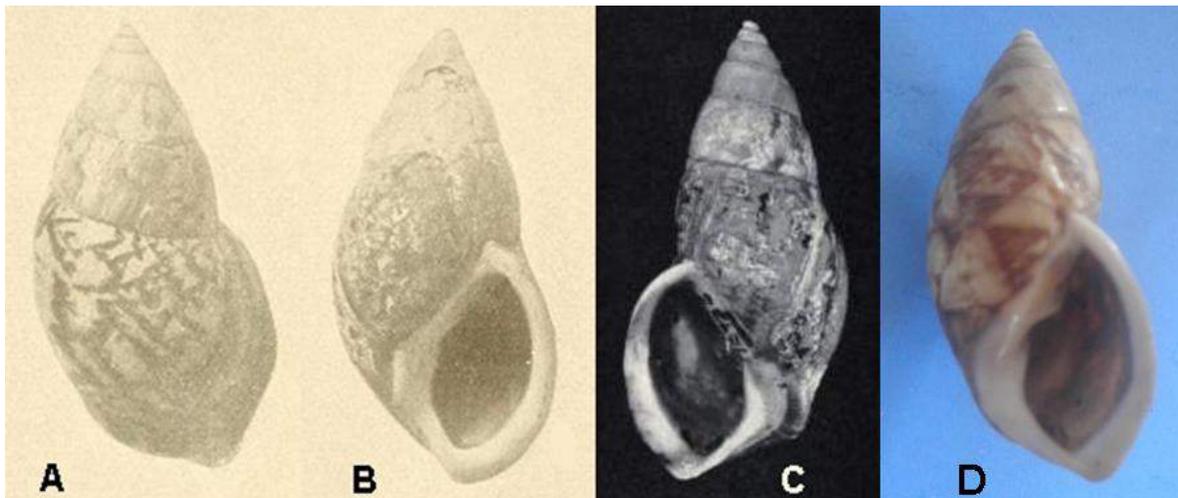


Figure 5. *A. (G.) b. bulowi* [not shown to the same scale]: **A–B** type shells figured by Fruhstorfer (1905; Taf. I, Fig. 2), **A** lectotype NHMUK 1910.12.30.98 and **B** paralectotype; **C** supposed “paratype” figured by Laidlaw and Solem (1961; fig. 37) CNHM 72436; and **D** shell showing a parietal ridge (JA).

Original Description (translated from Fruhstorfer, 1905)

Amphidromine shell of 7 flat whorls with a grey base colour, yellowish in younger specimens,

whereupon broad black zigzag lines crisscross unsystematically. The lip edge is wide and of a white colour. The subgenus' characteristic angle at the aperture shows up on the last whorl in front as a strongly protuberant keel.



Figure 6. Comparison of the paries and overall coloration of both subspecies [not shown to the same scale]: **A–B** *A. (G.) b. bulowi* (JP), **A** subadult shell and **B** adult shell; **C** *A. (G.) b. malalakensis* n. ssp. (paratype 2 JP); and **(5) D** patternless *A. (G.) b. bulowi* (JA) [Photos: **A & D** by John Abbas; and **B & C** by Jeff Parsons].

Shell Variation

Original colony had a majority of sinistral shells (Figures 5A–C). However, recent finds have only been dextral (Figures 5D, 6A, 6B, 6D & 7A–C). Paries colour changes with that of the penultimate whorl, salmon-buff or liver-brown, which varies in intensity. Shells are rarely patternless (Figure 6D) and very rarely showing a brown super medial band on the early teleoconch whorls (Figure 7A). Pattern coloration varies: the network-forming markings are chestnut, chocolate, hazel or blackish brown and often partially cover random, paler secondary markings, which are chestnut, tawny or dark ochre patches or longitudinal streaks. Occasionally shells have small white blotches and/or white lines bordering the brown lines (Figures 4 bottom & 7C). Ground of the last whorl is usually cream-coloured, rarely salmon-buff or liver-brown.

Rostrum varies in extension and depth, sometimes hardly protruding and very shallow (Figure 5B). The bent base of the columella is shorter than the top part in only the subadult (Figure 6A) and longer in all adult shells studied. Rarely mature shells may develop a ridge at the base of the paries (Figure 5D) and often the margin of the parietal callus is thickened (Figures 5D & 6B) and joined to the columellar margin. The subadult (Figure 6A) has no umbilicus visible and proof of its presence in juveniles is unavailable. *Amphidromus (G.) b. bulowi* shows the same variation as *A. (G.) b. malalakensis* n. ssp. for the columella's root and in the shape of the shell and parieto-labral tubercle. Aperture is narrow to moderately wide and oblong (Figures 5D & 6B) or subtrapezoid (Figures 5B–C) at a ratio of 10:7. Back of the outer lip varies: 1) grey (as per its face); 2) dark brown (continuation of markings; fig. 4 bottom); or 3) coloured as per ground of the last whorl (Figures 7B–C).

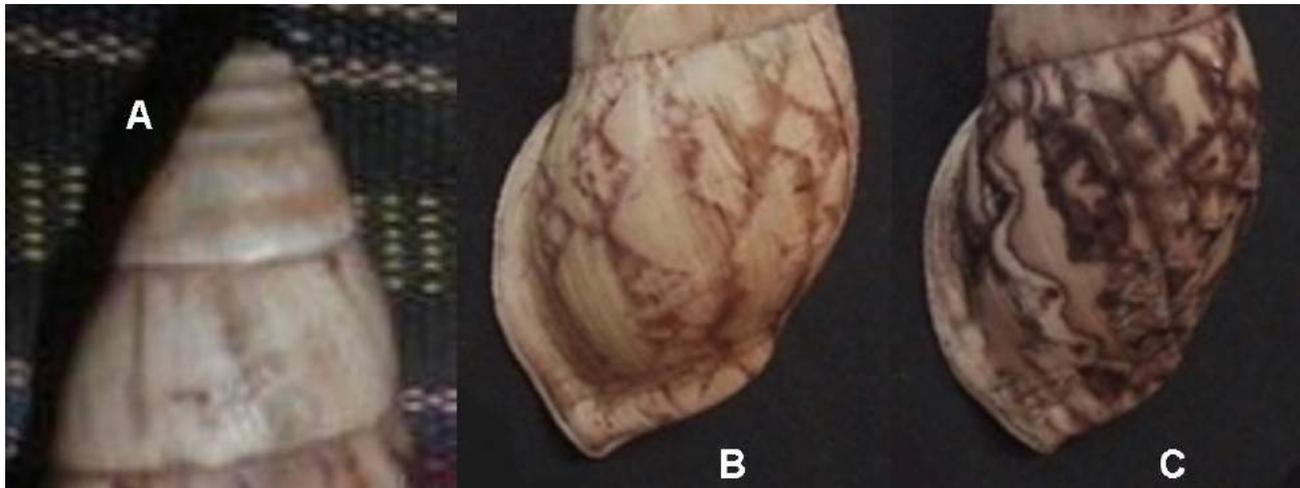


Figure 7. Coloration and pattern variation of *A. (G.) b. bulowi* (JA) **A** banded upper spire, **B** pale pattern elements and **C** dark pattern elements with some white borders [Photos by John Abbas].

DISCUSSION

The original population of *A. (G.) bulowi* was amphidromine and polymorphic. Volcanic activity from the twin volcano of Mt. Singgalang and Mt. Tandikat modified the soil, and hence the vegetation, on the residual hills and mounts of the western part of the Malalak valley. This valley is comprised of an andesitic rim of the Maninjau Caldera, Maninjau ignimbrite (c. 45000–55000 years old) covered with more recent tephra (ash deposits) from the twin volcano, which has part of its western flank also covered with tephra (Pribadi *et al.*, 2007). *Amphidromus (G.) b. malalakensis* n. ssp. represents ‘disruptive selection’ for individuals of one phenotype extreme that was better suited to a new ecological niche, such as that on Bukit Pandan, creating a habitat isolation event. This ‘ecotype’ formed a peripheral population on the boundary of a larger polymorphic population (parapatric distribution).

The snails’ arboreal habit allowed dispersal across the valley, even occasionally across the rivers and creeks present, and interbreeding occurred in a contact zone. Cycles of volcanic activity from the twin volcano, separated the

peripheral and main populations through destruction and modification of forest in the valley causing cyclic isolation and a peripatric distribution, thus establishing a ‘peripheral subspecies’. Contact between the two populations was re-established during periods of volcanic quiescence through vegetation regrowth on new soil. Increased human settlement and agricultural deforestation over the last 60 years has broken the snails’ dispersal paths across the valley, and mixing between the populations from Bukit Pandan and the twin volcano has ceased, creating an allopatric distribution.

Locals may not have collected sinistral specimens of *A. (G.) b. bulowi* due to shells being badly damaged, out of reach or simply absent where they have found live dextral snails. We are led to believe that they have only collected specimens on the eastern side of Mt. Singgalang, from forest above the locals’ crops to the summit (Figure 1, [blue dotted line](#)). If true, this suggests that *A. (G.) b. bulowi* has no real preference for vegetation type, and so it should be found anywhere on Mt. Singgalang and Mt. Tandikat above 1500 m altitude (Figure 1, [yellow dotted line](#)).

Only slight differences in animal coloration occur between the two subspecies. Optic and sensory tentacles are the same tone in *A. (G.) b. malalakensis* n. ssp. versus *A. (G.) b. bulowi* with paler sensory tentacles. The tail of *A. (G.) b. malalakensis* n. ssp. and often its neck show more flesh-pink than does those of *A. (G.) b. bulowi*. The body granulation in *A. (G.) b. malalakensis* n. ssp. is yellowish-orange or reddish-orange, yellowish-orange in *A. (G.) b. bulowi*. The mid-dorsal stripe is grey in both subspecies and also blackish in *A. (G.) b. bulowi*.

The two subspecies are easily separated based on shell coloration. Shells of *A. (G.) b. malalakensis* n. ssp. are ‘only dextral’ and chalk-white with pale grey and/or light buff to tawny primary pattern of anastomose lines, occasionally with fleshy-ochre or tan longitudinal secondary markings; white outer lip, columella and interior; and a buff-yellow to cinnamon-buff paries. In contrast, shells of *A. (G.) b. bulowi* are ‘rarely sinistral’ and have a salmon-buff or liver-brown spire and usually cream-coloured last whorl, with dark brown to blackish brown markings; greyish-white to pale grey outer lip, columella and interior; the paries is the same colour as the penultimate whorl and the back of the lip is grey, dark brown or the same colour as the last whorl. Shells of *A. (G.) b. bulowi* with periostracum still intact have the last whorl ground colour looks darker or pale brownish tinted, in contrast that of *A. (G.) b. malalakensis* looks off-white (fig. 4). The adapertural deviation in the anterior part or base of the columella, aperture angle and the keel angle varied for both subspecies, however, not significantly between them. Other shell morphometric data did not show any significant differences between them worthy of further mention.

The predictions of melanin pigments present in shells of both subspecies have been tabulated

(Table 1), and carotenoid-based red and yellow pigments are ignored. That data suggests the shell coloration of *A. (G.) b. malalakensis* n. ssp. is due to a basic lack of eumelanin, where small amounts form greyish primary markings and very small amounts create a greyish-white ground from the upper spire to the penultimate whorl. The white ground on the lower whorls is due to the absence of both eumelanin and phaeomelanin. By definition, these shells require a complete absence of both types of melanin to describe them as being albinistic (Hoekstra, 2006; van Grouw, 2012). Shells of *A. (G.) b. malalakensis* n. ssp. certainly have yellowish-brown markings and a brownish-yellow paries, most likely produced by phaeomelanin, so they are not albinistic shells. These shells are probably the result of a dilution gene, which causes an almost 100% reduction of eumelanin and leaves phaeomelanin unchanged, and best called “isabelline” shells (van Grouw, 2012).

A. (G.) b. bulowi is similar in shape to three Vietnamese species. *A. (G.) asper* Haas, 1934 has a larger shell with the same shell pattern, but has more convex whorls. The last whorl is very slightly flattened medially and subattenuated at the base, slightly compressed into a short rounded keel (holotype SMF 14428) or not (Figure 8A). The columella is vertical, straight to slightly twisted and sometimes bent briefly at its base toward the short spout; subtruncate in juveniles. The aperture is oblong and subcaniculate at the base (holotype) or not (Figure 8A), passing into a short wide basal spout. *A. (G.) mirandus* (Bavay and Dautzenberg, 1912) (Figure 8B) has a similar sized shell to *A. (G.) b. bulowi*, but differs in being thinner, pure yellow with green-line periostracum and has a wider, more protruding spout. *A. (G.) thachi* Huber, 2015 (Figure 8C-D) is also amphidromine, but differs in being a smaller, patternless white shell with a black

columella and black outer lip with a white border.

Current evidence suggests that *A. (G.) b. bulowi* is not present in western Malalak and continuation of agricultural deforestation will reduce the chance of such specimens being found there. Deforestation is worse on the eastern side of the valley, especially on Mt. Tandikat. The northern end of the valley is relatively untouched, but the physical

connection between the rim of the Lake Maninjau caldera and Mt. Singgalang has been severed by a road cutting. It is possible that both subspecies occur on the caldera rim near the road cutting, and *A. (G.) b. bulowi* may also occur on Mt. Marapi. *A. (G.) b. malalakensis* n. ssp. will remain extremely rare unless new colonies can be found. *A. (G.) b. bulowi* will still be rarely collected due to the ruggedness of its range, continued deforestation at lower altitude and predators.

Feature	outer lip, columella and interior	paries	back of outer lip	irregular, zigzag and/or branching lines	random longitudinal markings
<i>A. (G.) b. bulowi</i>	greyish-white** to pale grey*	liver-brown or salmon-buff	as per last whorl or stained chestnut	chestnut, chocolate, hazel or blackish brown†	chestnut, tawny, dark ochre, or absent
predicted melanin pigments present	a trace** or small* amount of eumelanin	eumelanin and phaeomelanin	eumelanin and phaeomelanin	eumelanin and phaeomelanin or only eumelanin†	eumelanin and phaeomelanin
<i>A. (G.) b. malalakensis</i> n. ssp.	white	buff-yellow to cinnamon-buff	white	pale grey* and/or light buff to tawny	fleshy-ochre, tan or absent
predicted melanin pigments present	none	phaeomelanin	none	minor eumelanin* or phaeomelanin	phaeomelanin
Feature	ground colour				
	early whorls	antepenultimate whorl	penultimate whorl	last whorl	
<i>A. (G.) b. bulowi</i>	chalk-white grading to greyish-white**	pale grey* becoming pale liver-brown or salmon-buff	liver-brown or salmon-buff ± cream-coloured patches	cream-coloured, rarely salmon-buff or liver-brown	
predicted melanin pigments present	none to a trace amount of eumelanin**	increasing amounts of eumelanin plus phaeomelanin	eumelanin and phaeomelanin patchy minor phaeomelanin	minor phaeomelanin or eumelanin and phaeomelanin	
<i>A. (G.) b. malalakensis</i> n. ssp.	as above	greyish-white**	greyish-white** and chalk-white patches	chalk-white	
predicted melanin pigments present	as above	trace amount of eumelanin**	trace amount of eumelanin** or none	none	

Table 1 Shell coloration comparison for both subspecies with predictions of melanin pigments present [Notes: pale grey* and greyish-white** are predicted to be the result of small/minor* and very small/trace** amounts of eumelanin].



Figure 8. Nearest relatives of *A. (G.) bulowi* [shown at approximately the same scale]: **A** *A. (G.) asper* Daklak province, Vietnam (JP; H 59.54 mm); **B** *A. (G.) mirandus* syntype MNHN 2046 (H 48.5 mm; photo by P. Maestrati MNHN); and **C–D** *A. (G.) thachi* paratypes figured by Huber (2015; **C** fig. 4, H 33.3 mm & **D** fig. 5, H 29.6 mm).

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