

Lectotype designation and descriptions of two new subspecies of *Amphidromus (Syndromus) laevus* Müller, 1774 (Gastropoda Pulmonata Camaenidae)

Jeff Parsons

47 Elizabeth Street, Aitkenvale, Queensland, Australia 4814; e-mail: jeffonese@yahoo.com.au

ABSTRACT

Amphidromus (Syndromus) laevus Müller 1774 (Gastropoda Camaenidae) was described without a type locality. Sampling made in Indonesia over the last 20 years has confirmed the presence of this species on Kisar Island (Pulau Kisar) and the Leti Islands (Kepulauan Leti) of the southwestern Maluku Province. Similar shells have also been found at Tutuala, Timor L'este. However, none of these specimens represents the nominal taxon and so its type locality is still to be determined. Sampling made in recent years on Roma (Pulau Romang) has not located any specimens of *A. (S.) laevus romaensis* Rolle, 1903. Herein a lectotype for *A. (S.) laevus* is designated and two new subspecies are described from the Leti Islands: *A. (S.) laevus janetabbasae* n. ssp. from Western Moa Island (Pulau Moa) and *A. (S.) laevus nusleti* n. ssp. found on Leti Island (Pulau Leti).

KEY WORDS

Amphidromus; subspecies; lectotype; taxonomy.

Received 22.02.2014; accepted 27.04.2014; printed 30.06.2014

INTRODUCTION

It has been 240 years since *Amphidromus (Syndromus) laevus* Müller, 1774 was first described, and its type locality still has not been determined. Previous authors usually stated imprecise localities for specimens of *A. (S.) laevus* (sensu lato), such as islands of Moluccas (Malaku Islands) (Fulton, 1896). Prof. von Martens (1867) said he had obtained this species while on Amboina (Ambon) from Mr. Hoedt, and other collectors indicated to him they had found it on the Tenimber (Tanimbar) Islands. In 1877 von Martens stated that Captain Schulze found it on Keffing Island close to Ceram (Seram), Moluccas. In addition to these imprecise or generic localities, Laidlaw & Solem (1961) added Java, Timor and Singapore; although they considered Keffing as a doubtful locality. No specimens of *A.*

(S.) laevus (s.l.) have been found on Ambon, Seram and the Tanimbar Islands in recent years, and here considered as doubtful localities until von Martens' specimens can be located and studied. This study has determined that this species does not live on both Java and Singapore, and so they are erroneous localities.

Specimens of *A. (S.) laevus* (s.l.) deposited in the Field Museum of Natural History (FMNH, Chicago, Illinois, USA) are from field trips in 1998. This confirms that this species lives on the islands of Leti, Moa and Lakor of the Leti Group (Kepulauan Leti), and Kisar Island (Pulau Kisar), southwestern Maluku Province (Provinsi Maluku) of Indonesia (Severns, 2006). Shells comparable to this species, *A. (S.)* cf. *laevus*, live near the eastern most point of Timor L'este at Tutuala, which is close to Leti and Kisar Islands (collections of

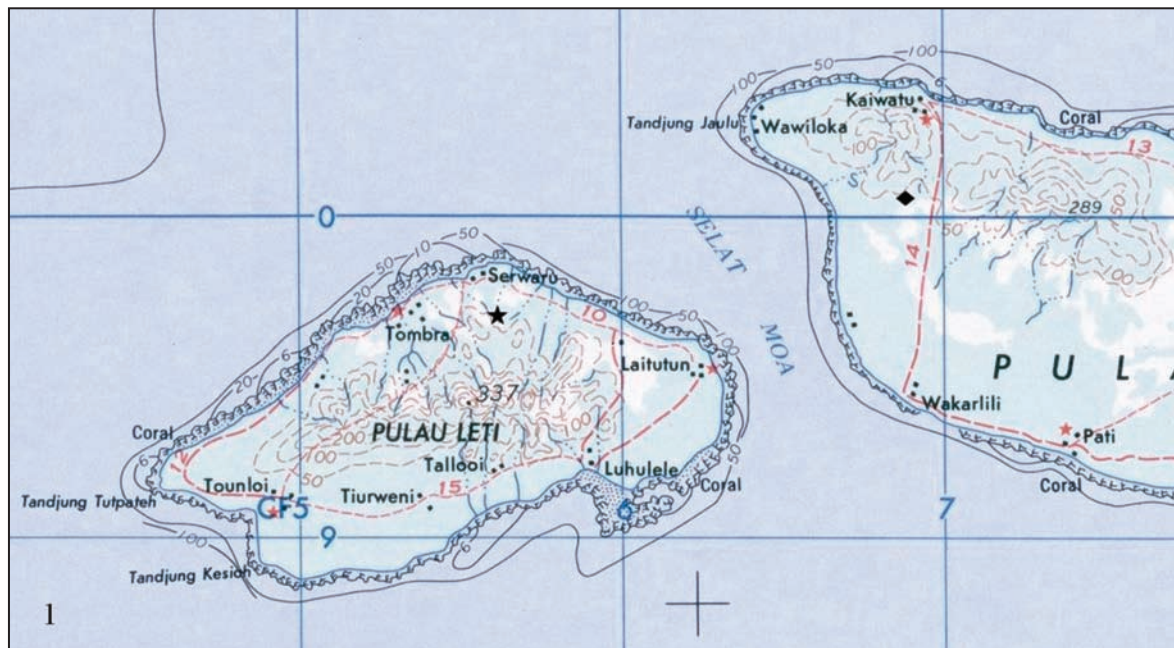


Figure 1. Map showing the approximate positions of the type localities for *Amphidromus (Syndromus) laevis nusleti* n. ssp. on Leti (black star) and *A. (S.) laevis janetabbasae* n. ssp. on Moa (black diamond) (modified from a map of “Palau Moa” including nearby islands: Army Map Service, Corps of Engineering (U.S. Army) 1963).

FMNH and JP). Field collections by John Abbas confirm *A. (S.) laevis* (s.l.) lives on Kisar (2008–2012).

Misidentification of other species as *A. (S.) laevis* (s.l.) has certainly occurred and led to erroneous locations. Misidentified species and shells labelled as “Timor” in museums are still under investigation and not discussed here.

In 2012, John Abbas organised field trips to Leti and Western Moa (see map, Fig. 1). These confirmed *A. (S.) laevis* (s.l.) lives on Leti and discovered a distinct population on Moa. Moa is the largest of the three main islands in the western part of the Leti group, separated by narrow channels from both Leti to the west (Moa Strait or Selat Moa) and Lakor to the east (Lakor Strait or Selat Lakor). A syntype of *Helix laeva* Müller, 1774 is selected as the lectotype of *A. (S.) laevis* and a detailed description is given. Detailed descriptions are also given for *A. (S.) laevis romaensis* Rolle, 1903 (lectotype) and *A. (S.) laevis kissuensis* Rolle, 1903 (lectotype), in addition two new subspecies are herein described as *A. (S.) laevis janetabbasae* n. sp. from Moa and *A. (S.) laevis nusleti* n. sp. from Leti.

MATERIAL AND METHODS

In the absence of preserved anatomical material or living animals for study, the descriptions are based on the morphological analyses of dry empty shells. Shells available for the present study are stored in the author’s private collection (including a single shell from Tutuala) (JP) and supplied by John Abbas (JA). Comparisons of some subspecies could only be made using digital images, supplied by museum staff, syntype of *A. (S.) laevis*, anonymous sources, *A. (S.) cf. laevis* from Tutuala and Lakor, and from online access of museum collections (lectotypes of *A. (S.) laevis romaensis* and *A. (S.) laevis kissuensis*). Müller’s measurement of “lin.” is assumed as the obsolete Danish line (English line), which is 2.18 mm (Stöver, 2001) and his measurements are converted accordingly. Relative sizes of shells for the subgenus *Syndromus* mentioned: small < 30 mm; medium 30–45 mm; large > 45 mm.

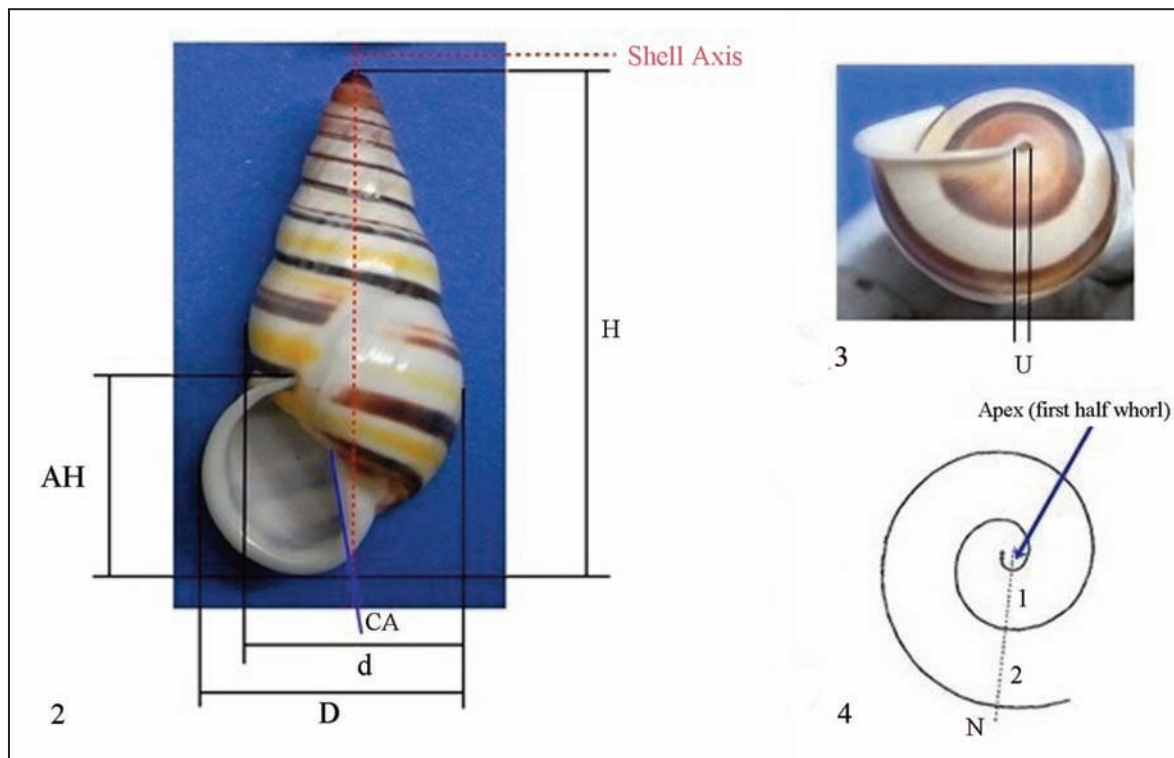
Shell sculpture was examined under low magnification (10x) using a jeweller’s loupe. All shells examined had formed a lip; those with a thickened lip were determined as adult and those with a thin

lip as subadult. The digital vernier calliper used to measure all shells has a resolution of 0.01 mm (Table 1). Measurements for specimens in digital images were calculated with the included scale bar. The five shell dimensions measured are (Figs. 2, 3): shell height (H), maximum shell width (D) and aperture height (AH) (measured including the lip); shell width above the aperture (d) and umbilical width across the opening (U). The columella angle (CA) was measured by placing a protractor over digital images of shells, with the shell axis as the zero degree point (Figs. 2–4). Number of whorls (N), include the apex and the teleoconch and counted precise to 0.125 ($\frac{1}{8}$ whorl) as per Haniel (1921) (Fig. 4). Measurement of the perch angle (PA) follows Dharma (2007). The ratios of shell height to shell width (H/D) and aperture height to shell height (AH/H) were calculated as indices of shell shape.

In order to make a comparison of banding patterns in *A. (S.) laevus*, von Martens (1867) counted only the dark bands on the last whorl and utilized a similar numbering system to that used for studying banding in pentataeniate (five-banded) Helicids

(e.g. Taylor, 1914; Cook & King, 1966; and Cook, 1967). Modifying his method for a pattern of six dark bands: the count starts below the suture from the highest of the superior bands (1 and 2), through the peripheral bands (3 and 4) to the lowest or basal bands (5 and 6). Each band present is given a number when present and a zero when absent. When all six bands are present, this gives a formula of 123456. Numbers placed in rounded brackets show two or more bands that have fused to form a wider single band, e.g. 1234(56). Two numbers underlined represent a band pair that has connected to form a two-toned band, e.g. 123456. Indistinct and partial bands are shown by a colon, e.g. 1:3456. Haniel (1921) used a slightly modified method by describing the pattern as seen on the last half whorl.

Two independent spiral band networks combine with a band around the umbilicus (circumumbilical band) to form the basic shell pattern as seen on the last whorl. Each network has three band zones occurring in alternate positions, with these named by position starting from below the suture working anteriorly toward the umbilicus. The first network has



Figures 2, 3. Shell dimensions, see Material and Methods for explanation of abbreviations, and Figure 4: method of whorl count (N) (Haniel, 1921)

Measurement	Species	<i>Amphidromus (Syndromus) laevus</i>					
	Subpecies	<i>laevus</i> (L)	<i>cf. laevus</i>	<i>janetabbasae</i>	<i>kissuensis</i>	<i>nusleti</i>	<i>romaensis</i> (L)
	Locality	unknown	Tutuala	Moa	Kisar	Leti	Roma
	Count	1	1	25	15	19	1
AH (mm)	range			12.06–17.04	12.26–15.47	12.36–16.59	
	average	11.83	18.54	15.05	14.03	14.04	18.27
AH/H (ratio)	range			0.36–0.47	0.38–0.44	0.41–0.47	
	average	0.45	0.42	0.43	0.41	0.44	0.41
CA (degrees)	range			5 to 20	6 to 18	5 to 20	
	average	5	5	10.56	11.47	10.11	5
N	range			5.625–7	5.25–6.875	5.375–6.5	
	average	5.50	6.5	6.25	6.25	5.888	7
PA (degrees)	range			16–25	18–24	18–24	
	average	NA	21	19.72	21.67	21.68	NA
H (mm)	range			27.59–44.21	29.57–40.52	27.07–36.30	
	average	26.26	44.23	35.19	34.45	31.72	45.06
D (mm)	range			15.35–19.69	14.93–20.41	14.77–21.26	
	average	14.69	21.78	17.73	17.68	16.89	22.95
d (mm)	range			12.30–16.50	13.09–16.91	10.73–17.51	
	average	12.71	18.19	14.92	15.12	13.62	18.70
H/D (ratio)	range			1.78–2.43	1.77–2.38	1.69–2.11	
	average	1.79	2.03	1.98	1.95	1.88	1.96
U (mm)	range			0.66–1.84	0.47–1.10	0.54–1.34	
	average	NA	0.71x1.48	1.20	0.93	0.98	NA

Table 1. Comparative shell measurements for the subspecies of *Amphidromus (Syndromus) laevus*. Data given as aperture height (AH); aperture height to shell height ratio (AH/H); columella angle (CA), offset to shell axis; whorl count (N), including apex (to nearest 1/8 whorl); perch angle (PA); shell height (H); shell width (D); shell width above the aperture (d); shell height to shell width ratio (H/D); and umbilical width (U). Note: L = lectotype; count is the number of specimens measured; and the umbilicus of *A. (S.) cf. laevus* (s.s.) from Tutuala is elongated whorl count (N) (Haniel, 1921)

generally pale coloured bands found below the suture (subsutural), middle of the upper half whorl (supermedial) and middle of the lower half whorl (submedial). The second network usually has dark coloured bands between the subsutural and supermedial bands (superior), near or on the periphery (peripheral) and between the submedial and circum-umbilical bands (basal).

According to the International Commission on Zoological Nomenclature (ICZN) code (1999), Article 72.4, Müller's type series includes one specimen (alpha) examined by him from the Spengler collection (Museo Spengleriano) and a cited specimen (beta) described and illustrated by Lister (1685). The colour variant beta described by Müller was unavailable for morphological examination or comparison through a photo.

A large part of Spengler's collection is deposited in the Zoological Museum, University of Copenhagen, Copenhagen, Denmark (ZMUC). Thanks to the help of Danny Eibye-Jacobsen, the specimen examined by Müller has been located in their museum. This shell was compared to the original description (Müller, 1774) and opinions of Chemnitz (1786), using photos supplied (ZMUC). This shell matches the dimensions given by Müller and the illustrations given by Martini (1777) and Chemnitz (1786), and is here considered as the actual shell seen by Müller. In absence of any other typical material with a known locality, under the terms of the ICZN code (1999), Article 74.7, this shell is here designated as the lectotype and discussed below.

Some taxonomic comments are required. Firstly, there has been some confusion made recently that the shells from Leti are a rediscovery of the nominal taxon (John Abbas pers. comm.). Those particular shells do not match Müller's type shell and they are herein described as a new subspecies. The nominal taxon remains an unlocalised species, since the labels found with the lectotype shed no light on the type locality. Secondly, certain shells from Kisar have been circulating among collectors incorrectly labelled as *A. (S.) laevus romaensis* Rolle, 1903 (John Abbas pers. comm.), which is a distinct form of its own and discussed below.

ABBREVIATIONS. Type material of the herein newly described subspecies of *A. (S.) laevus* have been deposited in the Australian Museum, Sydney, New South Wales, Australia (AM); the Natural

History Museum, London, England, UK (NHMUK); and Aquazoo/Löbbecke-Museum, Düsseldorf, Germany (LMA). Some additional type specimens belong to the private collection of John Abbas (JA) and private collection of the author (JP). Digital images of other type shells studied are from Senckenberg Naturmuseum, Frankfurt, Germany (SMF) and Zoological Museum, University of Copenhagen, Copenhagen, Denmark (ZMUC).

SYSTEMATICS

Family CAMAENIDAE Pilsbry, 1895

Genus *Amphidromus* Albers, 1850

Subgenus *Syndromus* Pilsbry, 1900

Amphidromus (Syndromus) laevus laevus
Müller, 1774

Helix laeva Müller, 1774: pp. 95–96, No. 293 (not illustrated)

EXAMINED MATERIAL. Digital images of a single syntype specimen from the ZMUC (Danny Eibye-Jacobsen), ex. Spengler Collection, and this is herein designated as the lectotype ZMUC-GAS-274 (Figs. 5, 6); dimensions: H 26.26 mm; D 14.69 mm; d 12.71 mm; and H/D of 1.79; type locality: unknown, original labels are without locality data (Figs. 8, 9).

DESCRIPTION OF THE LECTOTYPE. Shell small (26.26 mm high), sinistral, obliquely perforate (columnella hollow) and relatively solid. Shape ovate-conic with a moderately elongated spire. Surface is scarcely glossy; without macrosculpture. Microsculpture (as determined from digital images): protoconch (embryonic whorls) smooth; teleoconch (post-embryonic whorls) with numerous very fine growth threads with microscopic growth lines in the interspaces. Whorls about 5½, distinctly convex apically, next ones flatly convex and lowest a little convex; base angularly-rounded. Coiling is regular, the last whorl hardly descending in front. Suture weakly impressed apically, shallow on the teleoconch with a faint white marginal line. Remnants of a pale cream periostracum partially cover the last half whorl. Protoconch of about 1½ whorls, bulbous; infrasutural band opaque

cream, translucent pale flesh below. Apex (first half whorl) obtusely pointed and a little exsert; opaque cream (pale apical spot). Transition to the teleoconch is weakly distinguished by a change in whorl convexity and ground opacity. Teleoconch pale flesh apically, following whorls dirty white grading to white on the last.

Shell pattern is formed by a combination of two independent spiral band networks, each with three zones in alternate positions, and a circum-umbilical band. A white subopaque stripe (mora) about 1 mm wide, divides the bands clearly early on the penultimate whorl; and ends in an opaque greyish resting line, representing the former lip of a resting stage (see Figs. 5, 6). Using Haniel's (1921) method of describing the pattern as seen on the last half whorl, the band formula for this shell is 023456.

Aperture oblique, semioval and less than half of the total shell length (0.45); very pale yellow inside, clearly showing the external bands, but the violet ones are stained brown. Parietal callus scarcely perceptible, a thin colourless glaze; at the posterior end of its margin, a very short thickened lump adjoins the termination of the outer lip (parieto-labral tubercle), with nothing developed at the anterior end. Outer lip (labrum) white, very thin, subreflexed and barely expanded, white margined within the aperture. Columella white, narrow and thin-walled; subvertical, angled away from the aperture ventrally (abaperturally angled); twisted apically before straightening to join with the basal margin at an angle; weakly grooved at its root. Columellar margin narrow, revolute, dilated above and tapering to a narrow base, partially covering the narrow umbilicus. Interior of umbilicus (umbilical interior) blocked in ventral view.

ANIMAL AND SOFT PARTS. Details unknown.

DISTRIBUTION. Unknown.

BIOLOGY. Unknown.

COMPARATIVE NOTES. The *A. (S.) contrarius* group from West Timor, which includes the nominate form and two accepted subspecies, share some similarities with *A. (S.) laevus* (s.s.). Each of the *A. (S.) contrarius* subspecies has pattern varieties that are partially marked with continuous bands on the spire or lower whorls, but usually the bands are interrupted and indistinct or obsolescent.

Rarely some shells of *A. (S.) contrarius nikiensis* Rensch, 1931 develop banding like that of *A. (S.) laevus* (s.s.) (Fig. 18). Haniel (1921) indentified such shells as being *A. laevus* 'of the literature'. These *laevus*-like shells have 3 to 6 purplish or brown bands on the last whorl. The dark bands of *A. (S.) laevus* (s.s.) are reddish brown and violet bands on the exterior surface, and brown on the interior surface. Some shells of *A. (S.) contrarius nikiensis* have a similar disparity, with purple or greenish external markings appearing brown internally (Figs. 16, 19). The overall shell shape, structure of the lip and columella, and lack of a dark apex suggests *A. (S.) laevus* (s.s.) has a close connection to *A. (S.) contrarius nikiensis*.

The shape and form of the columella is also comparable to some species of the *A. (S.) inconstans* group, e.g. *A. (S.) inconstans* Fulton, 1898 and *A. (S.) wetaranus* Haas, 1912. These species have the root of the columella weakly impressed, as does *A. (S.) laevus* (s.s.). However, in *A. (S.) laevus* (s.s.) it is probably due to a lack of calcification and not a distinctive feature of the species. A faint yellow tint may occur on the columella and lip in shells of *A. (S.) wetaranus*. If the columella of *A. (S.) laevus* (s.s.) truly had a yellow tint when inspected by Müller, it has since faded to white.

Shells of *A. (S.) cf. laevus* from Tutuala, Timor L'este and *laevus*-like shells display another pattern variation. Both commonly have solid dark bands connected by alternating pale and dark blotches (maculated zones) on the spire and solid or split bands on the last whorl. In *A. (S.) cf. laevus* these maculated zones develop from bands with a paler central zone (two-toned bands), which becomes interrupted medially by pale coloured spots that fade-away before the last whorl. In the *laevus*-like shells, the maculated zones form by wide single superior and peripheral bands becoming interrupted medially by pale coloured spots, which are later stained pinkish brown. The dark blotches fade-away to leave a pinkish brown central zone between each pair of purplish or brown bands, creating two-coloured bands on the last whorl. These maculated zones are absent in *A. (S.) laevus* (s.s.), which instead has a few faded blotches discoloured to brown on the superior band; and the two peripheral bands suffer pigment leakage and become connected to form a two-toned band, pale centrally. All three taxa show variation in the band

colour (tonal variation) creating intermittently faded bands.

A. (S.) laevus (s.s.) is here judged as a distinct species. It can be separated from *A. (S.) contrarius nikiensis* by the following features: lip fused to the body whorl; a minute parieto-labral tubercle at the lip termination; continuous violet spiral bands; no solid flammules; no vague flammules formed from aligned dashes of interrupted bands; and nascent reddish brown subsutural, supermedial and submedial medial bands.

REMARKS. The measurements of the shell as positioned in the photos (Figs. 5, 6) give H 26.26 mm, D 14.69 mm and d 12.71 mm; and shell breadth (B) is 13.42 mm (Fig. 5). Here H and B approximately fit Müller's measurements of length 26.16 mm and breadth 13.08 mm, so it would seem Müller measured this shell in a similar position to that in figure 5. Original labels with the specimen (Figs. 8, 9) refer to the first illustrations made of it (Figs. 13, 14), with one label designating it as the type shell (Sp.) and states *Helix laeva* a Müll. (Fig. 9).

Müller described the colour of external surface as *lutescit*, meaning coloured like white clay or white with a muddy hue. Several times he described the colour of the columella as *lutea*, assumed to mean yellowish. The columella is now white with some dirt inside, which blocks any view inside the umbilicus to determine if it is white or tinged with the colour of the circumumbilical band. Müller may have been referring to this dirt giving the columella a yellow tint at the time. He also described the shell as having six brown bands, which must be referring to the bands as seen inside the aperture. Figures 5 and 6 show a subreflexed lip, so it is probably a subadult. The faint trace of a subsutural band is visible behind the lip in the original digital images, but lost in figure 6.

What is distinctive about this shell is the very pale yellow palatal wall, which may have been darker when collected in the 18th century. This feature is absent in subadults of the other subspecies of *A. (S.) laevus*. It is not peculiar to this species and is discussed further below.

This shell was not figured by Müller and first figured by Martini in 1777 (Figs. 13), who wrongly confused it with *Helix inversa* Müller, 1774 (*A. (S.) inversus*). Chemnitz later figured it in 1786 but only the dorsal view (Fig. 14). Three shells were located

in the ZMUC with a label identifies them as *Orthostylus laevis* (note "*laevis*" the typographical error taken from Pilsbry, 1900). Another label references the shell figured by Lister (1685) (Fig. 10), thus suggesting they are Müller's variation β . Photos taken by Tom Schiøtte (ZMUC) show them to be one adult and two juvenile shells indentified as *A. (S.) contrarius* Müller, 1774. This is possibly a case of the labels being mixed up with the wrong specimens. This would mean that Müller's variation β is still to be found.

Müller noted a shell that Gualtieri figured in 1742 (Fig. 11) is this species except for being dextral. However, he did not mention the fact that in the same volume he had named that particular shell as *Helix terebella* (species number 319, p. 123). It is now accepted as *Pyramidella terebellum* Müller, 1774 (Fig. 12), or as a synonym or subspecies of *P. dolabrata* Linnaeus, 1758. Müller (1774) placed the latter as species number 318 on pages 121-122, accepting both as being terrestrial. Müller's comparison between the two species must be due to the similarity in ground colour and banding pattern. The obvious differences are *P. terebellum* has a columella with three folds, a simple lip, a sharply attenuated spire and it is a marine species, not terrestrial like it was assumed to be at the time.

Chemnitz (1786) figured other shells that he identified as *A. (S.) laevus* (Tab. 111, fig. 941-948). His fig. 940 is Müller's type shell (Fig. 14) and shown marked with bluish (actually violet) and brown bands, yet he repeats Müller's description of it having six red brown bands. Yet for fig. 941 (Fig. 14), he clearly mentions that shell is white with three reddish or bluish (possibly violet) bands, which appears to mean reddish brown on the spire and bluish on the last whorl. When comparing both shells, there is enough resemblance to suggest they were possibly collected from the same population. Unfortunately, this shell is yet to be located and so was unavailable for this study. Chemnitz's fig. 949 is excluded because it is *A. (S.) furcillatus* Mousson, 1849. It does appear that subsequent authors (e.g. Reeve, 1849; von Martens, 1867 and 1877; and Pilsbry, 1900) have accepted Chemnitz's account of *A. (S.) laevus* as accurate, and have considered every shell similar in appearance to those he figured and described as being the same species.

Amphidromus (Syndromus) laevis romaensis
Rolle, 1903

TYPE MATERIAL. Lectotype designated by Zilch, 1953 (Laidlaw & Solem, 1961; p. 654), currently in the SM (Malakologie - SMF, 7574); ex. Sig. O. v. Moellendorff collection (ex. H. Rolle); dimensions: H 45.06 mm; D 22.95 mm; and H/D of 1.96; type locality: Roma (Romang) Island, northeast of Kisar and east of Wetar, Barat Daya Islands (Kepulauan Barat Daya), Southwest Maluku Regency, Maluku Province, Indonesia.

DESCRIPTION OF THE LECTOTYPE. Shell large (45.06 mm high), sinistral, obliquely perforate and very solid. Shape ovate-conic. Spire tall and regularly tapered. Surface is glossy. Macrosculpture (unmagnified): last whorl with occasional ridgelets, more numerous towards the lip. Microsculpture (as determined from digital images): protoconch smooth; teleoconch with growth lines and very fine growth threads. Whorls about 7, regularly increasing in convexity; base rounded becoming angularly-rounded behind the lip. Coiling is subregular with the last whorl descending toward the lip. Suture weakly impressed apically; shallow on the teleoconch with a thin white marginal line, more distinct on the last whorl. Periostracum thin, pale tawny and covers only the last whorl, thickening toward the lip. Protoconch is opaque, dome-shaped, about 1½ whorls; infrasutural band whitish; and pale yellowish below fading away on the second whorl. Apex opaque whitish (pale apical spot), obtusely rounded and protruding. Transition to the teleoconch is distinguished by a change in whorl convexity. Teleoconch pale yellowish apically, following whorls white without gradation to a yellow last whorl.

Pattern combination as per the nominal subspecies, but differs in band colouration and process of modification. A single whitish mora about 1 mm wide occurs close to the end of the penultimate whorl, preceding a very thin and quite distinct greyish resting line. The ground colour is rapidly changed to yellow and banding modified after the mora (post-mora modification) (see Fig. 21). The banding pattern as seen on the last half whorl, gives a formula of 023450.

Aperture oblique; strongly curved posteriorly, semicircular and about 41% of the shell height; yellow deep inside and weakly showing the external

bands, white callused toward the lip. Parietal callus very thin and colourless on the upper part; lower third is white and flatly thickened toward a lump beside the root of the columella (parieto-columellar tubercle). Outer lip reflected, expanded and thick; lower half with a vertically reflexed edge (rimmed). Columella white, thick, rounded and wide; subvertical and abaperturally angled ventrally; oblique and leaning outwards (proclined) laterally; forms a distinct angle where it joins the basal margin (columellar-labral junction); its base is gently curved out (excurved) and projecting a little. Columellar margin broad; a little dilated above and rolled over the narrow umbilicus. Umbilical interior is indiscernible in the digital images.

ANIMAL AND SOFT PARTS. Details unknown.

REMARKS. Laidlaw & Solem (1961: 654) considered it to be a variety of *A. (S.) laevis* based on the fact the distribution of the nominotypical form was not known. However, it is regarded by the SMF as being *A. (S.) laevis romaensis* Rolle, 1903. The shell is clearly marked as being the type shell indicated by the letter "T." inside the aperture along with its catalogue number (Fig. 21 centre). The "a" at the end of the catalogue number does indicate a second specimen, however, Rolle (1903) mentioned only one specimen and a search of the SMF database (SeSam - Forschungsinstitut Senckenberg 2013) only located a single specimen. There is no scale bar included in the digital images found on the SMF database (Fig. 21) and no measurements given either, so the measurements given by Rolle (1903) are accepted as accurate. After taking measurements from these digital images, it was concluded that Rolle measured "D" parallel to the suture and "H" perpendicular to that plane with the shell viewed ventrally (Fig. 21 centre).

A number of field trips to Roma over the last 3 years have not confirmed the presence of this subspecies (John Abbas, pers. comm. 2013). Laidlaw & Solem (1961, p. 573; FMNH, specimen CNHM 97362) mention another specimen; this shell was unavailable for this study. A further search on Roma is required to determine if it is still present or ever was found on Roma, may be it was found on a nearby satellite island instead of on Roma itself. For now, due to its distinct appearance the current status of this subspecies is accepted as valid.



Figures 5–7. Nominotypical subspecies A. (*S.*) *laevus laevus*: Figs. 5, 6. Lectotype, ZMUC-GAS-274 ex. Spengler Museum. Figs. 8, 9. The original hand written tags with the lectotype, both citing the illustrations by Martini (1777) and Chemnitz (1786), with (Fig. 9) identifying this specimen as the type shell, indicated by “Sp.” Fig. 7. Closer view of the parieto-labral node (circled) (Photos by Tom Schiøtte, ZMUC). Fig. 10. Shell figured by Lister 1685 with text (t. 33, f. 31). Fig. 11. Shell figured by Gualtieri (1742) with text (t. 4, f. M). Fig. 12. *Pyramidella terebellum* shown here for comparison (Maurice, 2013). Figs. 13, 14. Reproductions of original pre-1800 figures of *Helix laeva*. Fig. 13: lectotype by Martini (1777, Tab. I, p. 416, figs. 8–9). Fig. 14: figures by Chemnitz (1786, Tab. 111), (left) lectotype (Fig. 940) and (right) a shell very similar to the lectotype, Chemnitz Collection (Fig. 941). Note: shells are not shown on the same scale.

DISTRIBUTION. Known only from Roma (Romang) Island, northeast of Timor.

BIOLOGY. Unknown.

Amphidromus (Syndromus) laevus kissuensis
Rolle, 1903

TYPE MATERIAL. Lectotype designated by Zilch 1953 (Laidlaw & Solem, 1961; p. 633), currently in the SM (Malakologie - SMF, 7572), ex. Sig. O. v. Moellendorff collection (ex. H. Rolle); dimensions (see remarks): H 32.64 mm; D 17.77 mm and H/D of 1.84; type locality: Kisar (Kissu) Island, north of the eastern end of Timor Island, Barat Daya Islands (Kepulauan Barat Daya), Southwest Maluku Regency, Maluku Province, Indonesia.

DESCRIPTION OF THE LECTOTYPE. Shell medium (32 mm high), sinistral, obliquely perforate and quite solid. Shape distorted elliptic-pyramidal with a moderately long and tapered spire. Surface is shiny. Macrosculpture: lower teleoconch sporadically marked with growth threads. Microsculpture (as determined from digital images): protoconch almost smooth; teleoconch with numerous growth lines and no discernible spiral microsculpture in the digital images. Whorls about 6½, flatly to moderately convex on the spire; the last is strongly convex opposite the aperture forming a hump (laterally gibbose); base rounded to somewhat flattened and sack-like behind the lip. Coiling is irregular and distinctly distorted by the last whorl's gibbosity and descent toward the lip. Suture shallow, somewhat impressed apically and marked with a thin dull off-white edge. Periostracum absent, worn off or removed (see remarks below). Protoconch is dome-shaped with about 1½ whorls; subtranslucent pinkish brown. Apex obtuse, slightly exsert; black (dark apical spot), extending as an evanescent wedge and same-coloured infrasutural band. Transition to the teleoconch weakly distinguished by a change in whorl convexity and ground opacity. Teleoconch early whorls stained pinkish brown between the brown spiral bands and whitish above; the brown fades away on the fourth whorl; remaining whorls dirty white.

Pattern combination as per the nominal subspecies, except has different coloured bands. A pale

translucent grey weak mora occurs late on the antepenultimate whorl; about 1 mm wide and divides the bands cleanly (see Fig. 22). The band formula for the lectotype as seen on the last half whorl is 12(34)56.

Aperture is oblique, semicircular and about 45% of the shell height. Palatal wall colourless and pellucid, very clearly showing the external bands. Parietal callus is pale straw yellow, very thin and transparent; a small flattened parieto-columellar tubercle present on the parietal callus margin beside the root of the columella. Outer lip white, thickened, narrowly expanded and strongly reflected; external edge rimmed, distinctly so on the basal margin; raised a little above the suture at its termination (ascending termination). Columella white, thickened and wide; straight and oblique, abaperturally angled ventrally and proclined laterally; angular at the columellar-labral junction with its base projecting beyond it (extorted); weakly impressed at its root. Columellar margin wide; dilated above and tapering toward its base; curled over the narrow umbilicus, with its anterior edge distinctly recurved above it. Umbilical interior shows the ground colour of the last whorl, not stained by the circumumbilical band and clearly separate from it.

ANIMAL AND SOFT PARTS. Details unknown.

VARIABILITY. The spire is short to long with a tapered to somewhat turreted (subturreted) profile and the surface may be dull. Protoconch is almost smooth, occasionally with a few microscopic growth threads (microthreads). Teleoconch has a macrosculpture of growth threads throughout, or admixed with ridgelets on the lower whorls; and a microsculpture of numerous microscopic spiral striae (microstriae) overlain by very fine growth lines and microthreads apically, and coarser growth lines elsewhere. Generally, only one mora is present on the penultimate whorl, but commonly a second one may be present on the antepenultimate or previous whorl; and rarely absent or more than two present. The umbilicus is rounded (0.47–1.10 mm wide) or rarely elongated (0.51 x 0.97 to 0.56 x 1.22 mm).

Commonly shells have distorted lower whorls caused by irregular variation in coiling angle and whorl expansion. Distortion either affects just one part of the last whorl like in the lectotype (laterally



Figures 15–20. *A. (S.) contrarius nikiensis* from the NikiNiki area, West Timor showing variation of ground colour, pattern, interior, size and shape (JP). Fig. 15: brown flammulated form found closer to the coast and (Figs. 16 to 20) all found close to NikiNiki. Fig. 18: Haniel's *A. (S.) laevus* 'of the literature'. All shells except figure 17 have their periostracum still intact. Note: natural size of shells. Figure 21. Lectotype of *A. (S.) laevus romaensis*; SMF, Malakologie - SMF, 7574a (a composite of photos 19678-19680, SeSam - Forschungsinstitut Senckenberg 2013). Figure 22. Lectotype of *A. (S.) laevus kissuensis*; SMF, Malakologie - SMF, 7572 (a composite of photos 19675-19677, SeSam - Forschungsinstitut Senckenberg 2013).

gibbose), or affects both lower whorls (unequally gibbose). Coiling may also be subregular with the last whorl descending toward the lip and little or no distortion of the whorls. The dark apical spot varies as follows: apex to most of the first whorl darkly stained with black fading to brown or reddish purple at its edge; extended as per the lectotype to form a dark apical swirl, fading out toward or on the second whorl, or not extended.

Two distinct colour morphs occur, pallibicinctate and atrifasciate, with the appearance of the dark apical spot and protoconch colour varying between the morphs. Pallibicinctate refers to the two pale coloured bands generally present, one each encircling above and below the periphery. Since these shells lack the dark bands, the band formula is 000000. Atrifasciate refers to shells exhibiting dark coloured bands.

The umbilical interior is clearly separate from and never stained the circumumbilical band when present, and shows only the shell's ground colour. Rarely the teleoconch has a few scattered translucent grey flecks present. *A. (S.) laevus kissuensis* differs from the other subspecies by commonly having a third overlying band network present consisting of short to long segments of lime green lines superimposed upon the other bands and their interspaces. They appear in both colour morphs only on the last whorl, variable in length, and occasionally very slightly elevated above the shell's surface as spiral ribbons.

DISTRIBUTION. Known only from Kisar, north of Timor.

BIOLOGY. Unknown.

REMARKS. According to Laidlaw & Solem (1961, p. 633) the lectotype was first figured by Zilch (1953, pl. 22, fig. 10). They did not state any measurements of this specimen and incorrectly referred to it as the holotype (p. 633). There is no a scale bar included in the digital images (Fig. 22) in the SMF database (SeSam - Forschungsinstitut Senckenberg, 2013). The SMF classification for this taxon is accepted as *A. (S.) laevus kissuensis* Rolle, 1903. The shell is clearly marked as being the "type shell" indicated by the letter "T." inside the aperture along with its catalogue number (Fig. 22 centre). The "a" at the end of the catalogue number indicates a second specimen, and according to Rolle (1903) there were two syntypes.

The lectotype is a stocky, primarily white shell with brown bands and two very faded, subobsolete yellow supermedial and submedial bands and the subsutural band is absent. Yet Rolle mentioned black, brown and yellow spiral bands, which suggests the second shell had black bands with more distinct yellow ones. Based on this and after taking measurements from the digital image of the lectotype viewed ventrally (fig. 8 centre), this shell is most likely Rolle's larger syntype, since the calculated measurements closely match his: H 32 mm and D 17 mm. Rolle's second syntype has the dimensions of H 30 mm and D 16.2 mm.

Amphidromus (Syndromus) laevus janetabbasae
n. ssp.

TYPE MATERIAL. Number of shells examined: total 25; adult 22 and 3 subadult (very thinly reflected lips); Holotype: AM C.483433; Paratypes: LMA, (LMD/LÖB 133653a-b) (2 shells); AM C.483434 (5 shells); NHMUK 20120339 (4 shells); JAC (2 shells); JP (11 shells); dimensions: H 33.91 mm; D 17.21 mm; and H/D of 1.97; type locality: Moa Island, north-northeast of Timor Island, Southwest Maluku Regency, Maluku Province, Indonesia; found in villagers' plantations and the forest bordering them, on the eastern side of the road between the foothills to the north of Wakarlili on the southwest coast (Fig. 1).

OTHER MATERIAL. JA: from the type locality; 49 adult shells.

DESCRIPTION OF THE HOLOTYPE. Shell medium (33.91 mm high), sinistral, obliquely perforate and moderately solid. Shape ovate-conic with a moderately long spire, profile somewhat flattened; H/D ratio of 1.97. Surface is glossy; protoconch smoothish; teleoconch macrosculpture of growth threads on the lower whorls and occasional ridgelets on the last whorl; and teleoconch microsculpture of numerous spiral microstriae overlain by thin growth lines throughout and occasional microthreads apically. Whorls 6¼, slightly or moderately convex; a small section is a little swollen (subgibbose) just after the mora; base angularly rounded. Coiling is subregular, faintly distorting the lower whorls; last whorl descending toward the lip. Suture impressed apically, shallow below; bordered by a faint to bold white

marginal line. Periostracum removed in the holotype (see remarks below). Protoconch is rotund with about 1½ whorls; opaque cream infrasutural band is faint; ground subtranslucent pink; apex blunt, a little exsert. Apical spot pale, not blackened; whole apex opaque whitish. Transition to the teleoconch weakly distinguished by several microthreads.

Teleoconch ground stained pink apically, fading-away on the third whorl; remaining whorls whitish grading to yellow on the last; variously marked with pale, medium or dark coloured spiral bands, emerging on the second and third whorls forming a pattern combination as per the nominal subspecies, except more vividly coloured. A single translucent pale grey mora is present roughly mid-penultimate whorl; 1 mm wide, each side bordered by an opaque greyish resting line; it marks a rapid change in band colour and appearance (see Fig. 23). The holotype has the band formula of 123456.

Aperture is oblique with a perch angle of 19°; subovate and anteriorly subangular; AH/H ratio of 0.48. Umbilical interior white; moderately calcified and translucent, clearly showing the dark external bands. Parietal callus colourless; faintly calcified and imperceptible; a minute parieto-columellar tubercle present at the junction with the columella, fading as a curved trace along the parietal callus margin; and a minute parieto-labral tubercle adjoins the outer lip's termination. Outer lip has a white face and faded pale yellow inner margin with faded pale purple stains at both ends; thin, strongly reflected and narrowly expanded; face and external edge flat; posterior termination slightly ascending. Columella white; thickened, narrow and straight; oblique and abaperturally angled (9°) ventrally; subvertical and proclined laterally; angular at the columellar-labral junction with a slightly excurved base. Columellar margin white; curled over the umbilicus, partially covering it; face convex; cylindrically dilated, its base tapered. Umbilicus is round and narrow, 0.93 mm wide. Inner umbilicus tinged by the circumumbilical band.

ANIMAL AND SOFT PARTS. Unknown as all specimens were collected by locals for Mr. John Abbas and received as empty shells.

VARIABILITY. Shells are variable in shape, commonly ovate-conic, but also oblong (like that of *A. (S.) latestrigatus* Schepman, 1892) to elongate-tapering when distorted.

This species is very variable in the morphology of the aperture, palatal wall, outer lip, columella, columellar margin and base. The umbilical interior is very rarely yellow.

A well-developed parieto-columellar tubercle is generally a trace line or absent; uncommonly occurs as a thin curved line of callus in mature shells; and rarely a short smudge at the root of the columella.

A parieto-labral tubercle adjoined to the lip termination is rarely present, either a minute lump (as in the holotype) or an elongate lump a few millimetres long. The umbilicus is rounded and large for the group (0.66–1.84 mm wide) and rarely elongated (0.92 x 1.14 to 0.53 x 1.14 mm).

Faintly distorted subgibbose shells have less pronounced swelling of the lower whorls than *A. (S.) laevus kissuensis*. However, the subregular coiling in these shells causes a steeper descent angle of the last whorl, creating an appearance of greater distortion. Rarely true longitudinal distortion does occur (2 shells) where irregular coiling elongates the last whorl positioning it well below the periphery, thus exposing more of the previous whorl than usual. Coiling may also be regular or subgibbose without distorted whorls. Atrifasciate shells are the predominant form on Moa, with pallibicinctate shells being rare. Both morphs have a similar disparity in the colouration of the early whorls seen in *A. (S.) laevus kissuensis*.

In atrifasciate shells, the supermedial and submedial bands may brown, blacken or redden toward a mora and/or the lip, and the subsutural band rarely develops a brown tinge. The most constant band formulas are 020450 and 023450. All six bands are commonly present and rarely are five or all six partially absent on the last whorl, usually ventrally. The less common band formula of 000450 is comparable with two variations of *A. (S.) contrarius* Müller, 1774. The pure form of 000450 with bands 1 to 3 absent on the spire is quite rare. Commonly shells have other one or more bands on the spire that are lost randomly or after a mora and do not reappear on the last whorl. *A. (S.) contrarius* var. *suspectus* von Martens, 1864 displays pomegranate supermedial and submedial bands and the dark band formula of 000450, and rarely have bands 1 to 3 present on the uppermost whorls. *A. (S.) contrarius* var. *albolabiatus* Fulton, 1896 has only the pure form of 000450 and lacks the first network bands.

The external appearance of the lower whorls shows a wider range of shell colours created by the combination of periostracum, band and ground colour. The colour of the protoconch and first network bands is very variable. A variable dark apical spot is present or absent. A mora either marks a hiatus in the banding without modification of colour and/or pattern, or marks a rapid change. Additional shell pattern elements consist of dilution streaks and/or shadowy deepening streaks, usually on the last whorl.

DISTRIBUTION. Based on current material available, this subspecies is currently known only from type locality; it appears to be restricted to Moa, possibly found in the same vegetation type over the whole of the island.

BIOLOGY. Found on the leaves, limbs and branches of small trees and trunks of larger trees in deciduous broadleaf forest and villagers' plantations.

ETYMOLOGY. Named in honour of Mr. John Abbas' daughter Janet.

REMARKS. The holotype's minute parieto-labral tubercle is comparable to that of the nominal subspecies. Its labral inner margin stains are due to pigment leaked from the outer surface ground and bands. Its lip is thinner than average, but equal in thickness to a well-thickened lip seen in *A. (S.) contrarius* (s.s.). The periostracum when present covers only the lower whorls: thin, pellucid, dull; pale yellow to ochre; occasionally with darker or paler streaks toward the lip. These streaks tend to appear above the dilution or deepening streaks on the shell, which dilute or deepen the ground and pattern colour respectively. *A. (S.) kruijti* P. et F. Sarasin, 1899 has similar periostracal streaks. The parietal callus is colourless in fresh specimens, but becomes whitish and deteriorates in older empty collected shells.

The pale purple inner labral stains are comparable to those of other species. *A. (S.) kuehni* Moellendorff, 1902 has ruddy anterior and posterior stains (prominent externally, faded internally), and any faint yellow staining is from an external preapertural band showing through. In *A. (S.) annae* von Martens, 1891 the entire outer margin is reddish purple (claret when dark, or magenta when pale), across at least the lower lip face and sometimes faintly along the inner margin, with the deeper tones shining through to the outside. Shells are

excessively variable in colouring and banding, but commonly like that of the holotype. Compared to *A. (S.) laevus kissuensis* the supermedial and submedial bands are never obsolescent on the spire, but may appear faintly darker than the yellow or pale saffron ground of the last whorl. Inner wall is the preferred term to describe the exterior surface of the previous whorl inside the aperture.

The translucent flecks are generally greyish, rarely brownish, and sometimes have a same-coloured shadow. These particular flecks are comparable to a translucent brownish fleck and creamy shadow on *A. (S.)* cf. *laevus* from Tutuala; and the comet like markings of a black dot and yellow tail on *A. (S.) coeruleus* Clench et Archer, 1932.

***Amphidromus (Syndromus) laevus nusleti* n. ssp.**

TYPE MATERIAL. Number of shells examined: total 15 (adult); Holotype: AM C.483435; Paratypes: LMA, LMD/LÖB 133654a-b (2 shells); AM C.483436 (2 shells); NHMUK 20130070 (2 shells); JAC (2 shells); JP (6 shells); dimensions: H 32.33 mm; D 17.62 mm; and H/D of 1.83; type locality: Leti Island, north-northeast of Timor Island, Southwest Maluku Regency, Maluku Province, Indonesia; found in forest on the hills to the south of Sewaru village, which is on the northern coastline of the island near Cape Tutukei (Fig. 1).

OTHER MATERIAL. JP: 4 adult shells; 2 from the type locality and 2 from forest behind the beach near Cape Tutukei and Sewaru village. JA: from the type locality; 1) 27 adult and 2 juvenile non-atrifasciate shells; 2) 17 adult atrifasciate shells; 3) 6 adult mid-banded shells

DESCRIPTION OF THE HOLOTYPE. Shell medium sized (32.33 mm high), sinistral, obliquely perforate and heavily calcified. Shape ovate-conic; H/D ratio of 1.83. Spire moderately long and subturreted. Surface glossy; protoconch smoothish; teleoconch macrosculpture of growth threads on the lower whorls, and the last whorl also has numerous ridgelets and a varix and teleoconch microsculpture of crowded spiral microstriae crossed by growth lines and microthreads. Whorls 6; convex and gradually expanding; base angularly rounded becoming flattened behind the lip. Coiling is subregular; last whorl descends toward the varix and horizontal there-

after. Suture impressed apically and shallow on following whorls; bordered by a white marginal line. Periostracum removed in the holotype (see remarks below). Protoconch dome-shaped with steep sides, 1½ whorls; ground translucent pink; apex subangular, obtusely pointed and a little exsert. Apical spot dark; most of the first whorl stained black, becoming reddish purple marginally; extended along the sutural margin as a thin dark apical swirl, fading out on the second whorl. Transition to the teleoconch weakly demarcated by several microthreads. Teleoconch ground stained pink apically; second whorl whitened; fourth whorl stained very pale straw yellow, grading to saffron toward the varix and faded after it.

Pattern of spiral bands formed as per the nominal subspecies, but differently coloured and modified (see Fig. 24). The holotype has two incomplete bands and so a formula of 0::450.

Aperture is oblique, subovate and posteriorly rounded; perch angle 24° and AH/H ratio 0.49. Aperture interior thickly calcified, subopaque; whitish, a little glossy; external bands weakly visible, unmodified in colour. Parietal callus colourless; faintly calcified and inconspicuous; parieto-columellar tubercle is a small lump adjoined to the end of the columella margin's flange; parieto-labral tubercle is elongate, about 1 mm long. Outer lip white; moderately thickened, strongly reflected and moderately expanded; face flat; lower half of outer edge rimmed; posterior termination ascending a little. Columella white, thick and broad, a little twisted; subvertical and abaperturally angled (5°) ventrally; oblique and proclined laterally; angular at the columellar-labral junction, its base extorted. Columellar margin is white; jutted over the umbilicus, partially covering it; face convex and well thickened, forming a flange extending to its insertion point; cylindrically dilated and its base obliquely truncate with a subangular jut. Umbilicus is round and narrow, 1.08 mm wide. Umbilical interior partially tinged by the circumumbilical band.

VARIABILITY. Whorls are flattened to convex; sometimes the lower whorls are weakly to moderately swollen (subgibbose to gibbose), or just the last whorl is ventricose. Coiling is regular; subregular with the last whorl descending toward the lip; or irregular with the lower whorls unequally gibbose and faintly to distinctly distorted. Spire short

to long with a somewhat flattened to subturreted profile. Sculpture as per the holotype or a little rough locally, with occasional ridges or growth welts commonly on the last whorl, sometimes on the penultimate whorl and rarely on the upper whorls. The umbilicus is round, narrow to moderately wide (0.54–1.34 mm) and rarely elongate to rimate (0.65 x 1.18 to 0.35 x 1.10 mm). Umbilical interior always tinged by the circumumbilical band. Sometimes a single whorl forms the protoconch. Dark apical spot is large as per the holotype; or small with only the tip to whole apex stained black, extending outward a little while fading to brown or reddish purple at its edge.

Additional shell pattern elements consist of dilution or deepening streaks, sometimes the latter are browned or blackened on the last half whorl; and the teleoconch is rarely marked with translucent grey or brownish flecks. Resting lines are generally a growth stria, but sometimes form a ridgelet or swell up into a wide ridge formed from a former lip (true varix). On Leti, pallibicinctate shells are the predominant form, atrifasciate shells are uncommon and mid-banded shells are rare. There is a greater disparity in the colouration and form of the pallibicinctate and atrifasciate shells than that seen in *A. (S.) laevus janetabbasae* n. ssp. and *A. (S.) laevus kissuensis*. All three of these colour morphs may have the first network bands browned or blackened toward a mora and/or the lip, rarely reddened beforehand. The supermedial and submedial bands often appear faintly darker than or fade into the yellow or saffron ground of the last whorl.

A few shells have 6, 7 or 8 dark bands, but extra bands inserted into the pattern created these combinations. Only a single shell has the 000450 pattern with bands 2 and 3 on the upper whorls, a pattern more commonly seen in *A. (S.) laevus janetabbasae* n. ssp. Counting extra dark bands inserted into the pattern, a maximum number of 12 and minimum of 4 on the last whorl (subsutural, supermedial, submedial, and circumumbilical) bands present.

ANIMAL AND SOFT PARTS. Unknown as all specimens were collected by locals for Mr. John Abbas and received as empty shells.

DISTRIBUTION. Based on current material available, this subspecies appears to be restricted to Leti

and probably found in the same vegetation type over the whole of the island, including behind the beaches.

BIOLOGY. Found on the leaves, limbs and branches of small trees and trunks of larger trees in deciduous broadleaf forest and vine thickets.

ETYMOLOGY. The subspecies epithet is derived from Nusleti, a historical Letinese name of Leti Island (van Engelenhoven, 1997) and used here as a noun in apposition.

REMARKS. The holotype represents the average conchological features of the subspecies, and the average banding modification and pattern seen in the atrifasciate shells. It also has a true varix that occasionally develops in this subspecies. Its slate-coloured dark bands are not present in the other populations. Its parieto-labral tubercle is at full development for the subspecies. It has the following similarities with *A. (S.) laevus Janetabbasae* n. ssp.: columella and its margin are similarly formed; parieto-labral tubercle is equal at full development; and aperture is similar in shape. However, *A. (S.) laevus nusleti* n. ssp. tends to have an angular jut at the base of the columellar margin; parieto-columellar tubercle is a small lump or short ridge and never fades as a curved trace or forms a long ridge; and outer lip is opaque white with a flat or rimmed edge. Periostracum covers only the lower whorls when present: thin, pellucid, dull; and pale yellow to citron-ochre; sometimes with darker periostracal streaks towards the lip as in *A. (S.) laevus Janetabbasae* n. ssp.

Pallibicinctate shells may have no translucent grey morae present, or commonly have one or two present, 0.5–3 mm marked by an opaque resting line, and sometimes followed by a narrow whitish or yellowish post-marginal band. Occasionally wider multiple zones occur, composed of multiple very thin morae. One non-type shell has several deepening streaks stained with a reddish brown hue on the last half whorl. Overall these more or less yellow shells are comparable to *A. (S.) contrarius* var. *subconcolor* von Martens 1867, a nearly uniform yellowish white shell with two very faint yellow bands encircling the last whorl. However, it differs in the last whorl being darker yellow toward the base and faded above; and it has the same parietal tubercles and outer lip features as per *A. (S.) contrarius* (s.s.).

This subspecies also shows a rare intermediate form (6 shells), which shares features of both of the other two forms thus proving they are only colour morphs. These shells have a single very thin to thick dark, brown or blackish band at the periphery (mid-banded shells). The band is seen at the suture on the spire or not (1 shell). The band is absent on the last whorl in one shell, evanescent in another and faint to bold in the other four shells.

Compared to *A. (S.) laevus kissuensis* and *A. (S.) laevus Janetabbasae* n. ssp. the band patterns are extremely variable and more randomly developed; and partial bands are quite common, either incomplete or evanescent. The atrifasciate shells have less variation in band colour combinations than those of *A. (S.) laevus Janetabbasae* n. ssp., but there is greater colour variation in the ground and bands in its pallibicinctate shells. Compared to all the other subspecies, on average, this subspecies has a wider apex and a shorter spire for the same spire width; therefore, it has a greater spire angle. Partially interrupted bands caused by dilution streaks, tend to occur on the spire rather than on the last whorl. Such interruptions occur behind the lip on the only shell seen with all six bands present. The formation of the superior band and two-toned peripheral band is as follows: all three bands are brown on the second whorl, changing to slate on the third whorl; fade late on the penultimate whorl; and then deepen again early on the last whorl. On the fourth whorl, the space between bands 3 and 4 becomes grey, thus forming a two-toned band with a pale grey central zone, with the whole band intermittently faded.

DISCUSSION

Compared to the *A. (S.) contrarius* subspecies, the *A. (S.) laevus* subspecies differ by the supermedial and submedial bands displaying hues other than yellow; the submedial bands lack a same-coloured zone suffused over them; and the lack of axial or oblique flammules divided or not by a de-coloured (i.e. of the ground colour, whitish) or yellow supermedial band. In addition, the parieto-columellar tubercle is variably developed among the subspecies, never shelf-like; the lip termination is fused to the body whorl and the parieto-labral tubercle when present (minute or elongate

lump), so no gaps; and no canal beneath the suture inside the aperture. They also lack a pinkish brown medial zone between the bands of the superior and peripheral band pairs seen in the maculated zones of the *laevus*-like shells (Fig. 18). They may also display post-mora modification of pattern elements, also seen in *A. (S.) contrarius hanieli* Rensch, 1931 (and in *A. (S.) reflexilabris hanielanus* Rensch, 1931).

Even though some *A. (S.) contrarius nikiensis* shells have a similar colouration and band pattern (*laevus*-like shells figure 18) to the lectotype of *A. (S.) laevus laevus*, the latter has greater links to its subspecies. The data in Table 1 clearly show this, where all shell measurements are similar and no particular subspecies has anything outstanding dimensional features. However, some distinctive features can be noted: *A. (S.) laevus Janetabbasae* n. ssp.

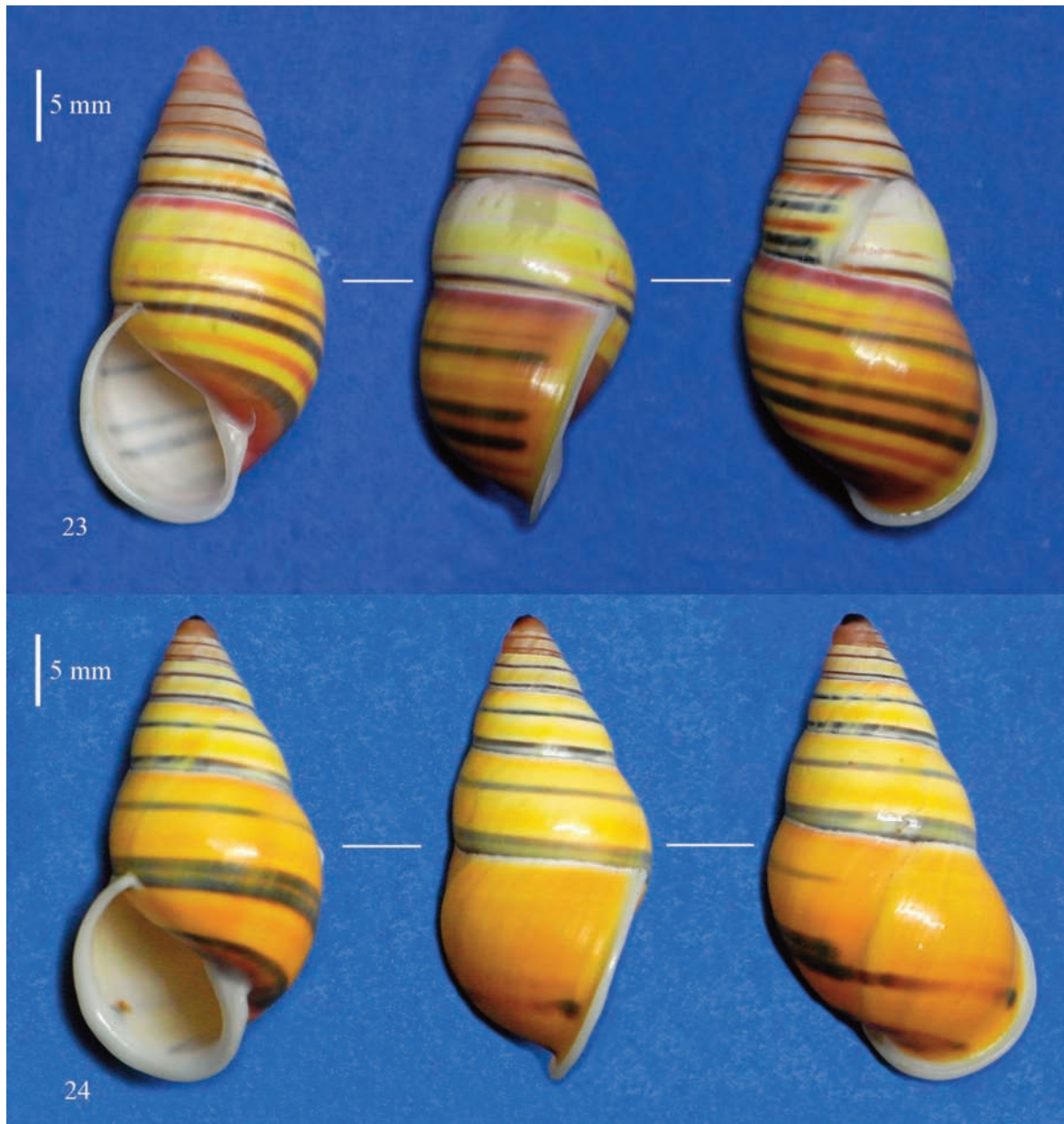


Figure 23. Holotype of *Amphidromus (Syndromus) laevus Janetabbasae* n. ssp.
Figure 24. Holotype of *A. (S.) laevus nusleti* n. ssp.

has a larger umbilicus; *A. (S.) laevus kissuensis* has a smaller aperture for the same sized shell; and on average *A. (S.) laevus nusleti* n. ssp. has the least number of whorls, a lower H/D ratio and smaller shells, with the largest shells coming from Moa, Roma and Tutuala. All subspecies have a AH/H ratio less than 0.5, plus similar columellar and perch angles.

The Kisar, Roma and Tutuala populations all have a rimmed lip, which is a distinctly reflected edge. For *A. (S.) laevus nusleti* n. ssp. the lip edge is variably flat or rimmed, with the degree of reflection dependant on lip maturity. In *A. (S.) laevus janetabbasae* n. ssp., only a few gerontic shells with greatly thickened lips have a weakly rimmed edge. The shape, colouration and pattern similarities of shells from Tutuala, Roma and Leti Islands (Leti, Moa and Lakor) suggest they originated from a common population. The *A. (S.) laevus romaensis* lectotype shows a great similarity in shape and pattern modification to some shells of *A. (S.) laevus janetabbasae* n. ssp., and the lack of a dark apex. But it has a stronger posterior lip curvature and a wide flattened parieto-columellar tubercle compared to *A. (S.) laevus janetabbasae* n. ssp., which has a thin curved line of callus (rarely a short smudge) and a more angular aperture. The same tubercle in *A. (S.) laevus nusleti* n. ssp. is short and thick, and a small-flattened lump in *A. (S.) laevus kissuensis*.

A. (S.) laevus kissuensis appears to have developed from a separate population to the other subspecies, differing in several features. Most shells have a whitish ground and the atrifasciate shells rarely having a yellow last whorl. The sub-sutural band when present is only ever yellow, of the same hue as the supermedial and submedial bands. The most distinctive feature is both colour morphs may display a third band network of lime green lines on the last whorl, something not seen in the other populations studied. The closest ties are between the subspecies from Leti and Moa, isolated only by a narrow sea channel. However, on Leti there is a predominance of the pallibicinctate shells compared to a scarcity on Moa. This suggests isolation was not only by a physical barrier but also by niche preference. Pallibicinctate shells prefer the drier and more open thorn forests on Leti, while atrifasciate shells prefer more shaded forests with a less open canopy on both islands.

Pallibicinctate shells of the above three subspecies are easily distinguishable. On Kisar, they are uncommon white shells with two or three yellow bands, often obsolescent with some shells grading to almost pure white; and may have lime green lines. Rare on Moa, shells with the last two whorls pale yellow, plus two or three pale to dark yellow bands, one or both may be partially tinged orange. Common shells on Leti, with the last two or three whorls of various yellow hues or grade to saffron; plus two or three pale to dark yellow or orange bands, often partially browned or blackened and rarely partially reddened. Sometimes the subsutural band is of different colour (rose or reddish orange) to the other two bands; and rarely has a narrow rose circumumbilical band (3 shells).

After a mora or growth flaw, atrifasciate shells of *A. (S.) laevus janetabbasae* n. ssp. commonly show a patchy loss and colour change (pied forms), or distinct and rapid colour change. The unmodified dark bands tend to be black or rarely brown. In the atrifasciate shells of *A. (S.) laevus nusleti* n. ssp. studied, unmodified dark bands are black, sooty, blackish brown, brown or slate; and band modification may occur before or after a mora, or occur randomly and gradually without a mora present. A single pied form from Leti has only the dark bands partially absent, which return changed to pink toward the lip. Both subspecies have a narrow to wide circumumbilical band that rarely fails to enter the umbilical interior, and the inner labral margin may have coloured stains, also seen in shells from Lakor. Either the purplish anterior stain is dominant and fades-away as the lip thickens (Lakor and Leti), or the longer yellow lateral stain is dominant and weak at maturity (Moa). Similar yellow staining seen in shells from Tutuala is in fact a preapertural band showing through from the outside.

A. (S.) laevus janetabbasae n. ssp. and *A. (S.) laevus nusleti* n. ssp. may have streaks that dilute or deepen the band and ground pigment, often faint or become distinct toward the lip. The Tutuala population has these too, and dilution streaks sometimes faintly or distinctly interrupt the bands on the spire. This happens in the other two subspecies too, but only as short sections of affected bands. Random partial dilution and deletion also forms interrupted bands. Dilution streaks often disturb the coloured suffusion on the last whorl, bleaching it thus showing an undertone (discussed below).

The medial zone of two-toned bands may suffer intermittent dilution, thus forming maculated zones of pale and dark blotches with dark borders. These maculated zones generally occur on the spire and are either short with weak randomly spaced small blotches (Leti and Moa), or long with wider alternating blotches (Tutuāla).

The first network bands may develop brown or black staining toward a mora and/or the lip in both colour morphs of *A. (S.) laevus nusleti* n. ssp. In atrifasciate shells of *A. (S.) laevus janetabbasae* n. ssp., only the supermedial and submedial bands have the same staining, commonly reddened too, and it rarely affects the subsutural band. *A. (S.) laevus* (s.s.) shows a similar feature, except the same bands are firstly invisible and then emerge on the last whorl stained brown. Only in *A. (S.) laevus janetabbasae* n. ssp. are these bands completely bleached to white after a mora and develop thin red or blackish borders. These band modifications are absent in the other populations. The subsutural band when present is generally the same colour as the other two bands in pallibicinctate shells, and commonly different in atrifasciate shells (magenta, red or rose).

Distortion of the lower whorls is similar in shells from Tutuāla, Leti and Kisar, although the latter have more gibbose whorls. *A. (S.) laevus janetabbasae* n. ssp. tends to have elongated distortion from a greater change in the coiling angle. A weakly developed shoulder and/or an obsolete subangular periphery on the last whorl may exaggerate distortion in *A. (S.) laevus nusleti* n. ssp.; a dark apical spot is always present in *A. (S.) laevus kissuensis*; very rarely absent in *A. (S.) laevus nusleti* n. sp. with only one shell known; present or absent in shells from Tutuāla, Moa and Lakor; and absent in *A. (S.) laevus* (s.s.) and *A. (S.) laevus romaensis*. Development of parietal tubercles varies among the subspecies, often absent or at least very weakly developed. A parieto-labral tubercle occasionally occurs in some shells from three populations: a minute lump (*A. (S.) laevus* (s.s.), Leti and Moa) or a small elongate lump perpendicular to the lip (Leti and Moa), and the latter is seen in some shells of *A. (S.) sinistralis* Reeve, 1849 and *A. (S.) centrocelebensis* Bollinger, 1918.

A parieto-columellar tubercle develops into one of four forms. The following is a comparison of *A. (S.) laevus* subspecies (locality of each is in brack-

ets) with other species that also develop each one of these. *A. (S.) latestrigatus* has a flattened lump (Kisar, Roma, Moa and Leti), except it is reddish purple. *A. (S.) beccarii* Tapporone-Canefri, 1883 and *A. (S.) annae* have a faint trace or long thin line (Moa). A long narrow ridge (Moa and Tutuāla) forms in *A. (S.) centrocelebensis* and *A. (S.) contrarius* (s.s.) (moderately developed). Lastly, a short narrow ridge (Leti) develops in *A. (S.) maculatus* Fulton, 1896 and *A. (S.) kuehni*. The same callosity when well developed in *A. (S.) contrarius* (s.s.) is like a ledge jutting out from the inner wall. Even this looks feeble compared to the ridge developed in *A. (S.) sinistralis*, which can be 1 to 2.5 mm thick rising to the same plane as the outer lip and appear as an extension of the columella.

Generally, *A. (S.) laevus kissuensis* has a white last whorl, rarely medium yellow. The other populations have various yellow tones on the last half to the lowest three whorls. Atrifasciate shells from Tutuāla show the greatest variation of the last whorl colouration, due to band pigment leakage suffusing across the whorl or as localised spiral zones. This suffusion is pink, magenta, purple, brown or greyish green, with an undertone of cream or yellow. *A. (S.) laevus janetabbasae* n. ssp. may have a pink suffused last whorl and a yellow undertone, or as pink, brown or pale reddish orange spiral or longitudinal suffusion zones. *A. (S.) laevus nusleti* n. ssp. shows only pink spiral suffusion zones.

According to Taylor (1914), an abrupt change in pigment colour can be due to a change in diet. Taylor also says if pigment-secreting cells are latent or undeveloped during early shell development, bands gradually or suddenly develop at the commencement of a growth period, or they show atrophy at the termination of a growth period that causes the partial or complete loss of bands during regrowth. This describes quite well some of the variation seen in the *A. (S.) laevus* group. However, the atrophy of the pigment-secreting cells may occasionally be a gradual process with the bands slowly fading-away. Taylor (1914) also discusses links for banding variation in *Theba pisana* Müller, 1774. He says in exposed habitats shells tend to have delicate linear banding that tends to be irregularly developed, while in less open and more shaded habitats shells have more distinct and better developed banding. This applies well with the banding of the *A. (S.) laevus* group, with the addition of the palli-

bicinctate shells being a form possibly adapted for exposed habitats.

Addition pertains to extra bands inserted into the pattern, not split from the main pattern bands, and occur as either short or long segments (partial bands). Division applies to main pattern bands that split into narrower bands or lines (bandlets). Width variation simply refers to different shells having either thin or thick bands, or in combination. Fusion ascribes adjacent bands gradually widening during development and connect to form wider bands. If fused bands dilate as well, then many bands may connect behind the lip to form a partially very dark shell (pseudomelanism). Spreading is band pigment leaked into the interspaces as stains, short streaks or connection of adjacent bands (two-toned bands), and widespread or zoned suffusion. Pigmentation variation involves intermittent fading of band and/or ground colour, occurring faintly along growth lines or wider marks along bands that may grade to maculated zones or even interrupted bands. In comparison, dilution and deepening streaks are pattern elements that modify the shell pigments more strongly. Reduction refers to indistinctly or irregularly developed bands, which are partially faded and those that gradually fade (evanesce) or gradually narrow before vanishing. Results of studies on other banded snails suggest that the banding pattern is probably under genetic control in this species as well.

The *A. (S.) laevus* group have another four types of pigmentation variation. Firstly, incomplete xanthism relates to the pallibicinctate shells where the yellow or orange bands are imperceptible on a same-coloured last whorl (Leti); and similarly coloured shells that have dark bands on the upper whorls (Tutuala). Incomplete albinism applies to almost pure white shells with very faint or obsolescent supermedial and submedial bands (Kisar); and shells with dark banded upper whorls and pure white lower whorls lacking first network bands (Tutuala). Partial leucism refers to the pied forms with short to long patch-like modification of some to all bands after a mora (Moa and Roma). It affects band colouration and presence, rarely affecting ground colour (Roma). No juvenile shells were available to show the pied modification affects bands on the base. Lastly, selective leucism pertains to the discolouration or dilution of band pigment without affecting the ground colour, for

at least part of the shell (Kisar, Leti, Moa and Tutuala). For example, the bands change from brownish to pinkish or from blackish to purplish, usually abruptly or gradually after a mora, less often randomly on the shell.

Overall the subspecies may share certain conchological features (e.g. weakly to distinctly abaperturally angled and/or proclined columella), but local modifications of others (e.g. parietal tubercles and sculpture) can be used to separate them in mature shells.

CONCLUSIONS

In their isolation, each island population of *A. (S.) laevus* has developed localised variations in shell pattern and minor differences in shell characters not found in other populations. Differences include, but are not limited to: apex colouration (black or dark apical spot, present or absent); colouration of the protoconch and lower whorls; thickness and reflection of the lip and columella; surface sculpture; and the development of parietal callosities. Variation in the banding occurs via a number of modifications, in terms of: addition, division, width variation, fusion, spreading, pigmentation variation, reduction, plus genetic control of the number of bands present.

Collectively these variations have developed a number of different subspecies, and the whole intention of this study was to show that. All of the above points show that the subspecies of *A. (S.) laevus* are a group of snails that are highly polymorphic in their shell colour and banding. This is especially the case for the Tutuala population. Due to the lack of study material, this study was unable to determine if shells like that of the *A. (S.) laevus laevus* lectotype occur on Lakor or at Tutuala. Further research is required to determine if they are separate subspecies. Knowledge of the conchological features and distinctive phenotypes created by local pattern variation, allows the subspecies to be distinguished in a mixed sample.

ACKNOWLEDGMENTS

I would like to thank John Abbas for the supply of type and comparative material for this study, and

for photos of shells in his collection. I owe a debt of gratitude to the following people: Danny Eibye-Jacobsen, Assoc. Prof., Curator (of the mollusc collection) and Tom Schiøtte for photos (ZMUC); Dr. Mandy Reid, Malacology Collection Manager for assistance in depositing type material (AM); Jonathan Ablett, Curator (of Non-Marine Mollusca and Cephalopoda, Division of Invertebrates, Zoology Department) for assistance in depositing type material and their photographic unit for photos (NHMUK); and Dr. Silke Stoll, Curator (of the mollusc collection) for assistance in depositing type material and photos (LMA).

REFERENCES

- Airaghi University of Texas Libraries. PCL Map Collection, Indonesia AMS Topographic Maps, Indonesia 1:250,000, Series T503, U.S. Army Map Service, 1954-, SC 52-2 Pulau Moa. Available at: <http://www.lib.utexas.edu/maps/ams/indonesia/txuoclc-21752461-sc52-2.jpg> [Accessed: 23 May 2013]
- Chemnitz J.H., 1786. Neues systematisches Conchylien-Cabinet. Neunten Bandes erste Abtheilung, enthaltend die ausführliche Beschreibung von den Linksschnecken oder von den verkehrtgewundenen Conchylien welche gegen die Gewohnheit aller übrigen ihre Mundöffnungen nicht auf der rechten, sondern auf der linken Seite haben. Mit vierzehn nach der Natur gemalten und durch lebendige Farben erleuchteten Kupfertafeln. Raspe, Nürnberg, [9], 1–151, Tab. 103–116.
- Cook L.M., 1967. The genetics of *Cepaea nemoralis*. *Heredity* 22: 397–410.
- Cook L.M. & King J.M.B., 1966. Some data on the genetics of shell-character polymorphism in the snail *Arianta arbustorum*. *Genetics*, 53: 415–425.
- Dharma B., 2007. Report on fossil *Amphidromus* and description of new species and new subspecies of recent and fossil *Amphidromus* from Indonesia (Gastropoda, Pulmonata: Camaenidae), *Schriften zur Malakozologie*, 23: 45–78.
- van Engelenhoven A., 1997. Words and Expressions: Notes on Parallelism in Leti, Cakalele, 8: 1–25.
- Fulton H., 1896. A list of the species of *Amphidromus*, Albers, with critical notes and descriptions of some hitherto undescribed species and varieties. *The Annals and Magazine of Natural History*, 17: 66–94, Pl. V–VII.
- Gualtieri N., 1742. Index Testarum Conchyliorum, quae adservantur in Museo Nicolai Gualtieri philosophi et medici collegiantii florentini Regiae Botanices Florentinae Academiae socii in Pisano Athenaeo Medicinae Professoris Emeriti, et methodice distributae exhibentur, Tabulis CX. Albizzini, Florentiae, I–XXIII, I–CX, Pl. I–CX.
- Haniel, C. B., 1921. Variationsstudie an timoresischen *Amphidromus* arten, *Zeitschrift für Induktive Abstammungs- und Vererbungslehre*, 25: pp. 1–88.
- International Commission on Zoological Nomenclature (ICZN), 1999, International Code of Zoological Nomenclature, 4th edition. The International Trust for Zoological Nomenclature, London; 1–140. Available at: <http://www.bio-nica.info/biblioteca/ICZNCode.pdf#8> [Accessed: 24 March 2013]
- Laidlaw F.F. & Solem A., 1961. The land snail genus *Amphidromus*: a synoptic catalogue, *Fieldiana (Zoology)*, 41: pp. 505–677.
- Lister M., 1685. *Historiae sive Synopsis Methodicae Conchyliorum, quorum Omnium Picturae, ad vivum delineate, exhibetur, Liber Primus, qui est de Cochleis Terrestribus; aere incisus, Sumptibus authoris; Susanna et Anna Lister Figures pin;* Londini: t. 33, f. 31.
- von Martens E., 1867. Preussische expedition nach Ost-Asien: nach amtlichen quellen. *Zoologischer Theil, Zweiter Band, Die Landschnecken, Mit XXII Illustrationen.* Verlag der Königlichen Geheimen Ober-Hofbuchdruckerei, Berlin. (R. v. Decker): *Bulimus laevus* pp. 359–362.
- von Martens E., 1877. Übersicht der während der Reise um die Erde in den -Jahren 1874–1876 auf S. M. Schiff *Gazelle* gesammelten -Land- und Süßwasser-Mollusken, *Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin* (1877 Mai): pp. 261–291.
- Martini F.H.W., 1777. Fortsetzung der vorläufigen Nachricht und Abbildung einiger linksgewundenen Schnecken, *Neue Mannigfaltigkeiten*. 4. Jg: pp. 416–418, Tab. I, figs. 8–9.
- Maurice J., 2013. *Pyramidella terebellum* (Müller, 1774) 1035, PYRAMIDELLIDAE Gray, 1840, Fiche 1, Mollusques de l'Île de la Réunion. Available at: http://vieocean.free.fr/mollusques/intro_frame.htm [Accessed 18 May 2013]
- Müller O.F., 1774. Vermium terrestrium et fluviatilium, seu, Animalium infusoriorum, helminthicorum et testaceorum, non marinorum, succincta historia, Volumen Alterum, Havniae et Lipsiae, apud Heineck et Faber, ex officina Mölleriana; *Helix laeva*: pp. 95–96, No. 293 (not illustrated).
- Pilsbry H.A., 1900. *Manual of Conchology, Structural and Systematic, with Illustrations of the Species, Series 2, Volume 13; Conchological Section, Academy of Natural Sciences of Philadelphia, Philadelphia; Amphidromus*: pp. 127–234, pl. 46–71.
- Reeve L., 1849. *Conchologia iconica, or, Illustrations of the shells of molluscous animals, Volume V, (September 1848); Reeve Brothers, London; Bulimus laevus* pl. 37, f. 216 b.

- Rolle H., 1903. Neue *Amphidromus*-Formen, Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 35 (No. 9, u. 10): *Amphidromus laevus* var. *romaensis* and *A. l.* var. *kissuensis* p. 157 (not illustrated).
- SeSam - Forschungsinstitut Senckenberg 2013, *Amphidromus (Syndromus) laevus kissuensis* Rolle 1903 Available at: <http://sesam.senckenberg.de/page/index.asp?objekt_id=562100&sprache_kurz=en> [Accessed: 24 March 2013]
- SeSam - Forschungsinstitut Senckenberg 2013, *Amphidromus (Syndromus) laevus romaensis* Rolle 1903 Available at: <http://sesam.senckenberg.de/page/index.asp?objekt_id=562100&sprache_kurz=en> [Accessed: 24 March 2013]
- Severns M., 2006. A new species and a new subspecies of *Amphidromus* from Atauro Island, East Timor (Gastropoda, Pulmonata, Camaenidae). *Basteria* 70: 23–28.
- Stöver C., 2001. Maße und Gewichte in alter Zeit. Available at: <http://www.rhaude.de/napoleon/mititaer/masse.htm> [Accessed 24 March 2013]
- Taylor J.W., 1914. Monograph of the land & freshwater Mollusca of the British Isles, Zonitidae, Endodontidae, Helicidae; Taylor Brothers, Publishers, Leeds; Helicidae: pp. 199–446, pl. XX–XXXV (includes distribution maps).