อนุกรมวิธานของหอยทากบกพัลโมเนตในสาธารณรัฐประชาธิปไตยประชาชนลาว

นายคำหล้า อินคะวิไล

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
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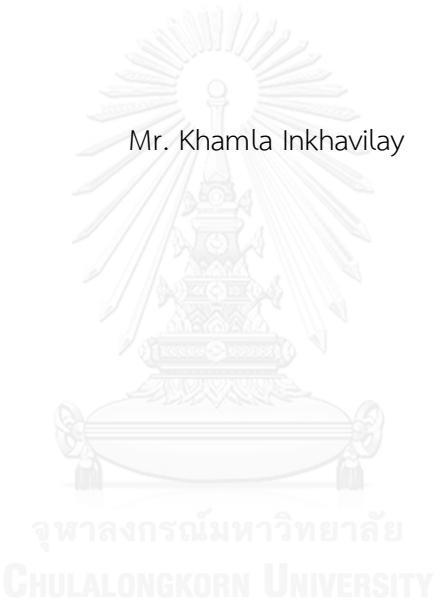
TAXONOMY OF TERRESTRIAL PULMONATE SNAILS IN LAOS

Mr. Khamla Inkhavilay



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คำหล้า อินคะวิไล : อนุกรมวิธานของหอยทากบกพัลโมเนตในสาธารณรัฐประชาธิปไตยประชาชนลาว (TAXONOMY OF TERRESTRIAL PULMONATE SNAILS IN LAOS) อ.ที่ปรึกษาวิทยานิพนธ์หลัก: ศ. ดร. สมศักดิ์ ปัญหา, อ.ที่ปรึกษาวิทยานิพนธ์ร่วม: ผศ. ดร. จิรศักดิ์ สุจริต, 182 หน้า.

ได้ทำการศึกษาอนุกรมวิธานของหอยทากบกพัลโมเนตในประเทศลาว ในปี ค.ศ. 2013 ถึง 2014 จากรายงานที่ผ่านมาพบว่า หอยทาก 76 สปีชีส์มีการรายงานและตีพิมพ์จากประเทศลาว การเก็บตัวอย่างได้ใช้พื้นที่สุ่ม 315 บริเวณ จาก 16 แขวง ซึ่งแบ่งเป็นสามพื้นที่ทางภูมิศาสตร์คือ เขตป่าเขาทางเหนือ เขตเขาหินปูนตอนกลาง และเขตป่าเบญจพรรณทางใต้ ทำการเก็บตัวอย่าง แล้วถ่ายภาพตัวอย่าง แล้วนำไปเก็บรักษาใน 70 % เอทานอล การจำแนกได้ใช้ลักษณะของเปลือก และอวัยวะภายในโดยเฉพาะอวัยวะสืบพันธุ์ ผลการศึกษาสามารถจำแนก และยืนยันหอยทากบกในประเทศลาวได้ทั้งสิ้น 112 ชนิด 50 สกุล จาก 17 วงศ์ และมีหอยทากบก 10 สกุล จาก 3 วงศ์ เป็นการรายงานครั้งแรกในประเทศลาว และเมื่อเปรียบเทียบกับจำนวนสปีชีส์ตามรายงานเดิม 76 สปีชีส์ พบว่าการศึกษาครั้งนี้พบที่เป็นรายงานครั้งแรกในประเทศลาวจำนวน 36 สปีชีส์ และได้ค้นพบและจำแนกเป็นสปีชีส์ใหม่อีก 10 สปีชีส์ จาก 4 วงศ์ (Camaenidae, Streptaxidae, Diapheridae, Vertiginidae) ซึ่งได้ตีพิมพ์ยืนยันการค้นพบนี้เรียบร้อยแล้ว การศึกษานี้ได้ทำการจำแนกประเภทหอยตามถิ่นที่อยู่อาศัย และพฤติกรรมที่สำคัญออกเป็น 4 ประเภทคือ 1) พวกอาศัยบนพื้นดิน 2) พวกอาศัยบนต้นไม้ 3) หอยนักล่า และ 4) หอยทากจิ๋ว หอยทากที่อาศัยบนพื้นดินที่โดดเด่นคือ วงศ์ Ariophantidae สามารถพบได้ทั้งสามพื้นที่ทางภูมิศาสตร์ *Cryptozona siamensis* และ *Hemiplecta distincta* คือสองชนิดที่โดดเด่น และพบในทุกพื้นที่ หอยทากจิ๋ววงศ์ Vertiginidae พบอยู่บริเวณเขตเขาหินปูนทางตอนเหนือ และตอนกลาง หอยต้นไม้สกุล *Amphidromus* จำนวน 14 สปีชีส์ พบทั้งสามพื้นที่ทางภูมิศาสตร์ แต่มีความหลากหลายของสปีชีส์ที่ต่างกันไปในแต่ละเขต หอยต้นไม้สองสปีชีส์ใหม่ที่ตีพิมพ์แล้วคือ *Amphidromus* (*Amphidromus*) *syndromoideus* และ *A.* (*Syndromus*) *xiengkhaungensis* พบทั้งตอนเหนือ และตอนกลาง หอยนักล่าวงศ์ Streptaxidae และ Diapheridae พบมีความจำเพาะในพื้นที่สูง จากจำนวนทั้งสิ้น 10 สปีชีส์ มีสี่สปีชีส์ใหม่ได้แก่ *Perrottetia unidentata, P. megadentata*, *Indoartemon diodonta* และ *Sinoennea euryomphala* พบที่บริเวณเขาหินปูนเป็นหลักของตอนเหนือ และตอนกลาง การค้นพบหอยทั้งสิ้น 112 สปีชีส์ เมื่อเปรียบเทียบกับพื้นที่ขนาดใหญ่และการค้นพบของประเทศใกล้เคียง ถือว่ายังมีจำนวนน้อยมากจำเป็นต้องศึกษาอย่างเข้มข้นโดยเฉพาะในฤดูฝนเพื่อตอบคำถามต่อไป

การวิเคราะห์ความสัมพันธ์ทางวิวัฒนาการ โดยใช้ลักษณะทางสัณฐานวิทยา ในหอยวงศ์ Ariophantidae ด้วยวิธีทาง Cladistic ในหอย 8 สปีชีส์ จาก 5 สกุล พบว่ามีความใกล้เคียงกับการจำแนกสัณฐานวิทยาที่ผ่านมามาก และแสดงความสัมพันธ์แบบวงศ์วานเดี่ยว หอยสกุล *Macrochlamys* และ *Sarika* แสดงความสัมพันธ์ใกล้ชิดกันด้วยค่า bootstrap 69% และหอยสกุล *Sarika* น่าจะถูกจัดไว้ในวงศ์ย่อย Macrochlamydinae

ภาควิชา ชีววิทยา ลายมือชื่อนิสิต .....

สาขาวิชา สัตววิทยา ลายมือชื่อ อ.ที่ปรึกษาหลัก .....

ปีการศึกษา 2559 ลายมือชื่อ อ.ที่ปรึกษาร่วม .....

5672803423 : MAJOR ZOOLOGY
KEYWORDS: TAXONOMY, LAND SNAILS, LAOS, DISTRIBUTION, CLADISTICS

KHAMLA INKHAVILAY: TAXONOMY OF TERRESTRIAL PULMONATE SNAILS IN LAOS. ADVISOR: PROF. SOMSAK PANHA, Ph.D., CO-ADVISOR: ASST. PROF. CHIRASAK SUTCHARIT, Ph.D., 182 pp.

Taxonomy of Laos' s terrestrial pulmonate snails has been carried out from 2013 to 2014 As from the previous records, 76 recognized species have been reported and published. There are 315 localities from 16 provinces dividing from three main geographic areas: the north montane forest, the central limestone karsts and the south deciduous forest. All those three areas have been intensively surveyed in the present study. All specimens were photographed prior to preserve in 70% ethanol. Shell morphology, soft parts anatomy especially the reproductive organs were used for identification. One hundred and twelve species that belong to 50 genera from 17 families were identified and updated. These included with the 76 previous recorded species, three new recorded families with ten genera were classified and incorporated in the total faunal record. Thirty six species were reported in Laos for the first time. Ten newly described species from four families (Camaenidae, Diapheridae, Streptaxidae, and Vertiginidae) were published. There are four snail types as classified from habitat and some distinct behaviour: 1) Ground dwellers 2) Tree dwellers 3) Carnivores and 4) Microsnails. The ground dweller Ariophantidae is quite dominant family which occurs in three regions. *Cryptozona siamensis* and *Hemiplecta distincta* are the best representatives. The microsnails family Vertiginidae are unique living on limestone habitats, were found mainly in the north and central of Laos. The fourteen species of tree snails *Amphidromus* were found also in three regions but slightly different in species composition. The two newly described, *Amphidromus* (*Amphidromus*) *syndromoideus* and *A.* (*syndromus*) *xiengkhaungensis* are from the north and central areas. The unique carnivorous Streptaxidae and Diapheridae perform high endemism. The total 10 species and the four newly described species, *Perrottetia unidentata*, *P. megadentata*, *Indoartemon diodonta* and *Sinoennea euryomphala* were collected mainly from limestone habitats of the north and the central areas. The total 112 species were very low compared to the large areas and the records from the nearby countries. The more critical surveys especially in rainy season might answer this question.

The phylogenetic relationship using cladistics analysis of 29 morphological characters in 8 species of 5 genera of the Ariophantidae performs the great congruence with morphological identification and exhibited monophyletic relationship. The genera *Macrochlamys* and *Sarika* showed a very close relationship by 69% bootstrap support. As from the analysis, the genus *Sarika* seemed to belong to the subfamily Macrochlamydinae.

Department:	Biology	Student's Signature	.....
Field of Study:	Zoology	Advisor's Signature	.....
Academic Year:	2016	Co-Advisor's Signature	.....

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Finally, I gratefully acknowledge my wife, daughters and son, brother and sister of warm heart family and all of my friends, who always gave great supports during this research.

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Chapter I

Introduction

The terrestrial snails are the second most diverse member of phylum Mollusca in term of described species. They have evolved as terrestrial animals from Carboniferous Period (354-290 mya), and the diversity markedly increased during the Cenozoic Era (Killeen et al., 1998, Lydeard and Lindberg, 2003). The land snails are phylogenetically distinct lineages and assemblages (Lydeard and Lindberg, 2003) which divided into two subclasses: Prosobranchia (snails that contain shell opercula, and gills locate in front of the heart) and Pulmonata (snails or slugs that possession of a complete lung sac with no opercula). The global assessment of land snail species richness estimated total global diversity ranged from 35,000 to 65,000 species (Barker, 1999; Bruggen, 1995; Bouchet et al., 2002; Stork, 1999). Despite the current records, there are approximately 25,000 species of described species. This indicates that there are about 10,000 to 40,000 undescribed species to be reported (Bouchet et al., 2002; Lydeard et al., 2004). In 2011, about 1,200 land snail species were included in the IUCN Red List of Threatened Species (Bauman, 1996; Clark and May, 2002; Coote and Loeve, 2003; Emberton, 1995). These numbers are nearly half of all known amphibian species, more than twice of shark and ray species, and nearly seven times of turtle species. This indicates relatively large number of land snails that listed as threatened status which absolutely reflected to the changing environments by both natural phenomena and human activities (Horwitz et al., 2001; Lawler et al., 2003; Moritz et al., 2001).

Laos locates in central of Indo-China, which is one of the world biodiversity hotspots with positioning in between the two large neighbors, Thailand and Vietnam. Laos area consists of the montane forest in the north, major limestone karsts and caves in the central, and the dipterocarp forest including over 4,000 riverine islands in the south. These make Laos still in pristine condition and diverse. The great numbers of endemic flora and fauna in Laos have been reported from several inventories (Davies et al, 2006; Robichaud et al., 2010). Therefore, the distinct taxonomic surveys are still very poorly practiced especially in all groups of invertebrates. In case of land snails, there are a few malacologists who conducted some inventory surveys and described

some species from Laos. By gathering all the relevant published literatures on land snails from Laos, there are less than a hundred species have been recognized so far. This number is contradicted to the minimum estimation of the land snail fauna both in Thailand and Vietnam, which consist of 500 to 1,000 nominal species (Panha, 1996; Schileyko, 2011). The discoveries of large numbers of small, narrow-range endemic land snail taxa (species, genus and family) in Thailand and Vietnam in the last two decades indicated that the land snail diversity in Laos should have comparable number of species to those areas.

The comprehensive land snail surveys of Indochina (especially in Laos) were initially conducted by various well-known European malacologists. Pfeiffer (1860) was the first who described 36 land snail species from Indochina in H. Cuming's collections, which contained 18 species from Laos. Later, 18 additional land snail species from Laos had been described from the same collections (Pfeiffer, 1863a, b). The French's malacologists also had a great contribution to land snail fauna that recorded in Indochina. For examples, Crosse and Fischer (1863, 1891) reported terrestrial molluscs, mainly in Laos and Vietnam, with 5 species were from Laos, and Morlet (1892) reported 8 species from Luang Prabang and Bolikhamxay. Ancey (1898) and also Dautzenberg and Fischer (1905) reported several land snail species from Indochina, which included 12 species described from Luang Prabang. Möllendorff (1897) described 13 species of land snails collected from Boloven plateau in Champasak. The comprehensive checklist of land snails in Indochina was compiled for the first time by Fischer in 1891, which included 54 land pulmonate snail species from Laos. Since the latest publications in the late eighteen century, the fundamental knowledge on Laos land snail fauna has not yet been improved and there are still no additional species have been reported. In nineteen century, Panha (1996) started to publish the checklist of 221 land snail species in Thailand which 26 species also occured in Laos. Later, Panha-et al., (2002), Panha and Burch (2005) described 3 microsnails from Vientiane. Later, two species of the tree snails from Savannakhet were reported by Lehmann and Maassen in 2004 and Sutcharit and Panha in 2006. In 2011, Schileyko published a checklist of the terrestrial pulmonate snails including 477 species from Vietnam, of which 40 species are from Laos. In summary, approximately 70 to 100 land snail species

have been recognized so far. This is quite contradicting from the above mentioned of highly habitat diversities, comparing with several hundred species from the neighboring countries such as Thailand and Vietnam.

The phylogenetic analysis by using morphological characteristics has been used in all snails. There are some recent studies that proved to be great references for systematic interpretation, for examples, Hausdorf (1995) reported the relationship between *Dyakia* and other genera in the family Dyakiidae by discussing the relationship of the genera *Dyakia* and *Rhinocochlis* that are sister groups and sinistral coiling is a synapomorphic characters of both genera, and the long ectocones of the radular marginal and the keeled body-whorl might be synapomorphies of *Rhinococilis nasuta* with subgroup of *Dyakia*.

Objectives

1. To study and revise taxonomy of the terrestrial pulmonate snails in Laos
2. To determine the distribution of each snail family.
3. To reconstruct phylogeny of a large snail family Ariophantidae using morphological characteristics.

Anticipated benefit

The terrestrial land snail taxonomy can be used in biodiversity conservation and management in Laos.

Chapter II

New species of micro snails from Laos (Pulmonata: Vertiginidae and Diapheridae)

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Abstract

Five new species of minute vertiginid and diapherid snails, each with the characteristic apertural barriers for their genera (angular and parietal, collumellar and palatal), are described. *Paraboysidia anguloobtusus* **n. sp.** has a high conical shell, shouldered whorls with impressed sutures, and very fine spiral striae. The aperture contains seven robust barriers with distinct, blunt, angular lamella and a curved upper palatal plica. *Paraboysidia paralella* **n. sp.** has a high, ovate, embryonic shell with a very fine porous structure. The aperture contains five robust barriers, including angular and parietal lamellae located parallel to each other, a knob-like basal lamella and a short and thickened supracolumella tooth. *Gyliotrachela plesiolopa* **n. sp.** has a turbinated shell, embryonic whorls with a pitted, porous sculpture, sutures impressed and the final whorl ascends and expands to a trumpet shaped aperture. There are five major apertural barriers: angular, parietal, columellar, upper and lower palatal, plus six small additional plicae: two infraparietals, two interpalatals and two infrapalatals. *Angustopila singuladentis* **n. sp.** has a conical spire, suture depressed, embryonic with a porous sculpture, shell sculpture with fine spiral threads. The shell aperture contains one thick and strong parietal lamella. *Sinoennea euryomphala* **n. sp.** has a high pupa-shaped shell, aperture opened narrowly vertically and subcircular shaped. The shell aperture contains large and strong parietal-angular lamellae, bifurcation palatal and columellar lamellae. Umbilicus widely opened.

Key words limestone, taxonomy, Laos, Vertiginidae, Diapheridae

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Introduction

Terrestrial pulmonate snails in Indochina exhibit a wide size range of shell dimensions, ranging from over 70 mm diameter in *Hemiplecta distincta* to less than 5 mm in the so-called micro-snails. The Vertiginidae and Diapheridae are the major families of pulmonate micro-snails in the region and range from the east of India to Southeast Asia including southern China and Japan (Panha and Burch, 2002; Zhang et al., 2014). Micro-snails are most diverse and abundant on limestone and many are restricted to limestone, leading to local endemism and highly restricted distribution ranges (Jochum et al., 2014). Over a hundred nominal species of pulmonate micro-snails have been recorded from Indochina (Panha and Burch, 1999a, 2000 2001, 2005; Pilsbry, 1917; Richardson, 1988; Thompson and Upatham, 1997). Most are known from Myanmar, Thailand and Vietnam, with only one species each of *Krobylos* Panha and Burch, 1999, *Paraboysidia* Pilsbry, 1917 and *Sinoennea* Kobelt, 1904 being reported from Laos (Maassen, 2008; Panha et al., 2002; Panha et al., 2004).

The significant proportion of records are from areas nearby to Laos, such as Thailand, rather than from within Laos, as indicated in several publications compiled in Burch and Panha (2002) and Panha and Burch (2005). The recorded data are comprised of 63 species of micro-Vertiginidae belonging to twelve genera (*Acinolaemus*, *Anauchen*, *Antroapiculus*, *Aulacospira*, *Boysidia*, *Gyliotrachela Hypselostoma*, *Krobylos*, *Montapiculus*, *Paraboysidia*, *Pupisoma* and *Systenostoma*), and two species of micro-Diapheridae belonging to the genus *Sinoennea*. The present paper describes an additional five species from Laos in a different genus *Angustopila* and re-arranges the family classification to Vertiginidae and Diapheridae.

Materials and Methods

Field collections were performed in northern Laos at Houaphane, Luang Phrabang and Luang Namtha Provinces from September 2013 to December 2014 (Fig. 2.1). Various habitat types of limestone karst, including caves, were searched for samples. Leaf litter and topsoil were also collected and searched. Specimens were identified based on Bavay and Dautzenberg (1908, 1912); Benthem Jutting (1949); Maassen (2008); Panha and Burch (2005); Pilsbry (1917) and by comparison with type material in the Chulalongkorn University Museum of Zoology.

Specimens were carefully cleaned with a delicate brush under a stereomicroscope and further examined under scanning electron microscopy (SEM; JEOL, JSM-5410 LV). To maximize resolution of informative characters, drawings were made with the aid of camera lucida. Cell'D imaging software was used for determining the shell height (H) and width (W) measurements.

The terminology of the shell shape and shell sculpture follows that of Pilsbry (1917), Benthem Jutting (1949), Schileyko (1998) and Panha and Burch (2005). The nomenclature of the shell apertural barriers follows that of Pilsbry (1917): A = angular; B = basal; C = columellar; c^1 = supracolumellar; c^2 = subcolumellar; c^2 and $c^{2.1}$ = subcolumellar; i^1 = infraparietal; i^2 = suprapalatal; i^3 = interpalatal; i^4 = infrapalatal; lPl = lower palatal; P = parietal; uPl = upper palatal.

Institutional abbreviations: **CUMZ**, Chulalongkorn University Museum of Zoology, Bangkok, Thailand; **NHM**, The Natural History Museum, London; **NUOL**, National University of Laos, Vientiane, Laos; **SMF**, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main.

Systematics

Family VERTIGINIDAE Fitzinger, 1833

Subfamily GASTROCOPTINAE Pilsbry, 1918

Remarks: The family treatment of the three following genera: *Paraboysidia* Pilsbry, 1917, *Gyliotrachela* Tomlin, 1930 and *Angustopila* Jochum et al., 2014 (=*Systenostoma*) is still controversial. Originally, Pilsbry (1917) recognized and classified them within the family Pupillidae, subfamily Gastrocoptinae. Later, Zilch (1959) proposed the new classification by placing *Paraboysidia* and *Gyliotrachela* in the Hypselostomatinae and *Angustopila* in the Aulacospirinae, both of which were previously in the subfamily Chondrininae. Schileyko (1998) rearranged and recognized these three genera into the same family Hypselostomatinidae by combining two of Zilch's subfamilies. The most recent classification by Bouchet and Rocroi (2005) rearranged the previous treatment from both Zilch (1959) and Schileyko (1998) as synonyms of the Vertiginidae: Gastrocoptinae. Therefore, in this paper, we follow the most recent classification by placing *Paraboysidia*, *Gyliotrachela* and *Angustopila* into the family Vertiginidae, subfamily Gastrocoptinae.

Genus *Paraboysidia* Pilsbry, 1917

Boysidia (*Paraboysidia*) Pilsbry, 1917: 174, 201. Schileyko, 1998: 137, 138. Schileyko, 2011: 2.

Bensonella (*Paraboysidia*)—Zilch, 1959: 164.

Paraboysidia—Benthem Jutting, 1949: 5, 18. Panha and Burch, 2005: 113, 115.

Type species. *Boysidia paviei* Bavay and Dautzenberg, 1912, by original designation.

Remarks

This genus is characterized by having a minute, conical shaped shell, aperture adnated to the last whorl, and peristome continuous and usually expanded. Apertural barriers with parallel and separated angular and parietal lamellae, and other lamellae may be present or absent. *Boysidia* Ancey, 1881 and *Anauchen* Pilsbry, 1917 differ from *Paraboysidia* by the genus *Boysidia* having fused angular and parietal lamellae to form a bi-lobed lamella; while the genus *Anauchen* performs only parietal lamella (Pilsbry, 1917; Benthem Jutting, 1949).

Currently, the genus *Paraboysidia* is comprised of 17 nominal species, which range from southern China to Indochina and peninsular Malaysia. Five species were reported from Indochina (three species from Vietnam and two species from Laos) and nine species were reported from Burma and Thailand (two species from Burma and seven species from Thailand) and the other 3 species were reported from Penninsula Malaysia (Pilsbry, 1917; Yen, 1939; Benthem Jutting, 1949; Panha and Burch, 2005; Maassen, 2008).

Paraboysidia gittenbergeri **Maassen, 2008**

Figures 2.1, 2.2A–C, 2.4A; Tables 2.1, 2.2

Paraboysidia gittenbergeri Maassen, 2008: 237-239, figs 5, 6.

Type locality: 500 m SE of Phou Lek Village, Oung Pra Ngiene,

Vieng Phouka, Luang Namtha, Laos.

Material examined

Limestone outcrop at Vieng Sawang Village, Vieng Phouka District, Luang Namtha Province, Laos (20° 41' 14.9" N, 101° 4' 8" E), 687 m above mean sea level (amsl): CUMZ 7055 (1 shell, Fig. 2.2A), CUMZ 7056 (16 shells).

Remarks

No living snails were found; only empty shells were collected from the top soil at limestone outcrop bases near the type locality (Figs. 2.1 and 2.2A–C). This species clearly differs from *P. robusta* (Bavay and Dautzenberg, 1912), *P. lamothei* (Bavay and Dautzenberg, 1912) and *P. pavei* (Bavay and Dautzenberg, 1912) in shell size and apertural barriers. In comparison, *P. robusta* has a sub-quadrate aperture, angular and parietal lamellae that are not separated, infraparietal lamellae present with oblique columella lamella and strong upper palatal plica. *Paraboysidia lamothei* has a smaller shell (height 3 mm) with nine apertural barriers, infraparietal and angular lamella, very strong seated at the edge of the peristome and running downwards almost adnated to the upper palatal plica. Likewise, *P. pavei* has a much smaller shell (height 1.8 mm) with seven apertural barriers, infraparietal lamella and a larger subcolumella (Tables 2.1 and 2.2).

***Paraboysidia anguloobtusus* Inkhavilay & Panha, n. sp.**

Figures 2.1, 2.2D–F, 2.4B; Tables 2.1, 2.2

Type material. Holotype CUMZ 7057 (H = 1.9 mm, W = 1.6 mm; Figs. 2.2D–F).
Paratypes CUMZ 7058 (8 specimens in ethanol), NHMUK (2 shells), SMF (2 shells).
Type locality. Limestone wall outside of Kao Rao Cave, Vieng Phouka District, Luang Namtha Province, Laos (20° 43' 30.1" N, 101° 9' 4.3" E), 732 m amsl

Diagnosis

Paraboysidia anguloobtusus n. sp. has a high conical shaped shell with a straightened spire and impressed sutures. The protoconch has spiral striae. Aperture heart shaped, peristome with seven major apertural barriers (angular, parietal, columellar, subcolumellar, upper and lower palatal and suprapalatal). The angular

lamella is blunt, parietal and columellar lamellae form an embayment. Upper palatal plica bends in a deeper location, lower palatal distinct forming an embayment with basal lamella.

Description

Shell minute, high conical, with 4¾ whorls, straight-sided spire, shell height 1.8–2.1 mm and width 1.4–1.6 mm (Fig. 2.2D). Embryonic shell about 1½ whorls with defined spiral incised lines (Fig. 2.2F). Teleoconch sculpture with thin irregular growth lines and very fine spiral striae. Last whorl largest, shouldered; impressed sutures. Peristome complete and adnate to last whorl. Aperture circular and open vertically. Six apertural barriers; angular, parietal, columellar, subcolumellar and lower palatal plica are well developed. Palatal edge at peristome invaginated making a distinct barrier. Angular lamella thickened, blunt at the tip, terminal located almost at apertural edge towards inside with slightly curved, upper palatal plica located deeper inside aperture. Parietal and angular lamellae spaced; parietal large and strong, located deeper from peristome; columellar lamella thickened and located firmly at peristome edge, subcolumellar plica also prominent. Upper palatal plica short, thin, curved and seated lower than peristome edge. Lower palatal plica long and stout, reaching to aperture margin; suprapalatal plica short and thin; upward nearly meets parietal lamella. Umbilicus narrow and deep.

Derivation of name

The specific name "*anguloobtusus*" is derived from the Latin word "*angular*", meaning "tooth", and "*obtusus*", meaning "blunt", and refers to the blunt angular lamellar tip, which is the prominent character of this species.

Distribution and habitat

This new species were only found at the type locality. Snails occur on limestone wall, crevices with moss on the rock surface near the entrance of the cave and covered with thick vegetation (Fig. 2.1).

Comparisons

Paraboysidia anguloobtusus n. sp. differs from *P. paviei* and *P. lamothei* in having blunt, angular lamella and a different shell shape. In comparison, *P. paviei* has infraparietal lamella seated closed to the parietal and angular lamellae, the latter of which are not curved, the suprapalatal lamella are absent and the peristome lip is less concaved, umbilicus widely opened. For *P. lamothei*, it has a larger shell size, inconspicuous growth line striae, more apertural barriers, infraparietal present, angular lamella, very strong seated at the edge of the peristome, and running downwards almost adnated to the upper palatal plica.

Paraboysidia anguloobtusus n. sp. differs from *P. nabhitabhatai* Panha and Burch, 2002, *P. wangviangensis* Panha and Tongkerd, 2002, *P. pangmapaensis* Panha and Burch, 2001 and *P. gittenbergeri* Maassen, 2008 in having a different shell shape, number of apertural barriers and their forms. In comparison, *P. nabhitabhatai* has a larger parietal lamella and the twisted, angular lamella has two cusps but is not curved, suprapalatal lamella is absent, and the embryonic shell is smooth. *Paraboysidia pangmapaensis* contains eleven apertural barriers with upper palatal plica marginal and bifid, while *P. wangviangensis* has a smaller shell, a lower number of barriers, the largest and strong marginal angular lamella extends into the aperture and downwards closed to upper palatal plica, forming an angulo-palatal embayment. *Paraboysidia gittenbergeri* has a larger shell, descending aperture, fewer barriers and the angular and parietal lamellae locate downwards parallel to the upper and lower palatal plicae (Table 2.2).

***Paraboysidia paralella* Inkhavilay & Panha n. sp.**

Figures 2.1, 2.3A–C, 2.4C; Tables 2.1, 2.2

Type specimens. Holotype CUMZ 7059 (H = 2.7 mm, W = 2.3 mm; Figs. 2.3A–C).

Paratype CUMZ 7060 (42 specimens in ethanol), NHMUK (2 shells), SMF (2 shells).

Type locality. Limestone wall near the entrance of Kao Rao Cave, Vieng Phouka District, Luang Namtha Province, Laos (20° 43' 30.1" N, 101° 9' 4.3" E), 732 m amsl.

Diagnosis

Paraboysidia paralella n. sp. has an elongate-heliciform shell shape. Embryonic shell large, perforated, with about 2¼ whorls. The aperture is semicircular shaped. Apertural barriers contain five major teeth (angular, parietal, columellar and upper and lower palatal) with one small supracolumellar tooth and one basal tooth located in the deep of aperture. Peristome lip wide reflected.

Description

Shell high spired, elongate-heliciform approaching oval with 4¾ whorls, straightened spire with deep sutures, shell height 2.3–2.9 mm and width 1.6–2.3 mm (Fig. 2.3A). Embryonic shell is large with about 2½ whorls and a perforated surface (Fig.2.3C). Teleconch sculptured with thin and irregular growth lines. Seven apertural barriers: angular, parietal, columella and upper and lower palatal lamellae well developed. Angular lamella thickened, located almost at the apertural margin and extended downwards into aperture; parietal thickened and seated slightly deeper, parallel to angular lamella. Columellar lamella well developed; strong and oblique located at the apertural margin, oblique towards inside; a small supracolumellar lamella located deeper over columella lamella. Small convex knob-like basal plica

located deeper inside. Upper and lower palatal plicae stout located inside after aperture (Fig. 2.3B, 2.4C). Umbilicus widely opened.

Derivation of name

The specific epithet *paralella* is from the Latin "*parallel*", referring to the angular and parietal lamellae that are located parallel to each other.

Distribution and habitat

The new species, *P. paralella* n. sp., is only found at the type locality, and is sympatric with *P. anguloobtusus* n. sp. The snails occurred on limestone walls and crevices with a moss covered rock surface near the entrance of the cave (Fig. 2.1).

Comparisons

Paraboysidia paralella n. sp. differs from *P. pavei*, *P. lamothei* and *P. pangmapaensis*, the other large-shell snails in this genus. It has a shell height of over 2.3 mm, as same as *P. lamothei,* but contains several types of apertural barriers. In comparison, *P. pavei* has a smaller shell (height 1.8 mm), subtriangular aperture, supracolumellar and basal plica are absent, and the umbilicus is widely opened. *Paraboysidia lamothei* has a larger shell (height 3 mm), nine apertural barriers, parietal lamella very strong and bended downwards with the upper palatal plica to form a rounded sinulus. *Paraboysidia pangmapaensis* has a smaller shell (height 1.7 mm), eleven apertural barriers, shell sculptured with space spiral striae, and large, twisted parietal lamella (Table 2.2).

Genus *Gyliotrachela* Tomlin, 1930

Gyliauchen Pilsbry, 1917: 210.

Gyliotrachela Tomlin, 1930: 24 [nom. nov.]. Zilch, 1961. Schileyko, 1998: 140, 141.

Type species. *Hypselostoma hungerfordianum* Möllendorff, 1891: 337, by original designation.

Remarks

The genus *Gyliotrachela* Tomlin, 1930 is characterized by having trumpet shaped tuba and a conical spire. Last whorl is straightened, short to long with regular, ascending or descending angles. Peristome expanded; angular and parietal lamellae separated and parallel. This genus differs from *Hypselostoma* Benson, 1856 in having separated angular and parietal lamellae, while these lamellae fused into a single or concrescent in the *Hypselostoma* (Pilsbry, 1917; Panha and Burch, 2005).

Gyliotrachela is comprised of over twenty species recorded in Southeast Asia, West and North Australia (Schileyko, 1998), and over ten species have been recorded from Indochina especially in Thailand and Vietnam (Panha and Burch, 2005; Schileyko, 2011). No *Gyliotrachela* species has been reported so far from Laos.

***Gyliotrachela plesiolopa* Inkhavilay & Panha n. sp.**

Figures 2.1, 2.3D–F, 2.4D; Tables 2.1, 2.2

Type specimens. Holotype CUMZ 7061 (H = 1.9 mm, W = 3.5 mm; Figs. 2.3D–F).

Paratypes CUMZ 7062 (28 specimens in ethanol), NHMUK (2 shells), SMF (2 shells).

Type locality. Limestone outcrop in Naweed Village, Viengxay District, Houaphane Province, Laos (20° 22' 37.3" N, 104° 16' 43.2" E), 695 m amsl.

Diagnosis

Gyliotrachela plesiolopa n. sp. has a shell with slightly ascending tuba (about 20°). Protoconch distinct with perforated sculpture, teleoconch with a fine transverse or growth line or striae. Peristome has five major spinosed dentitions: angular, parietal, columellar and upper and lower palatal. There are two additional infraparietal plicae

and one interpalatal plica. The angular lamella locates slightly superior outer, parietal lamella locates a bit lower inside.

Description

Shell minute, trumpet tuba, about four whorls and spire with short conic, shell height 1.5–2.2 mm and width 2.6–3.5 mm (Fig. 2.3D). Embryonic shell about 1½ whorls, with perforated sculpture (Fig. 2.3F). Teleoconch with fine and irregular growth line. Last whorl enlarged, with short and slightly ascending tuba, shouldered and weak angular; other whorls rounded. Sutures well impressed and deep. Aperture rounded; peristome free, continuous and broadly expanded. Apertural embayments are well developed, circular angulo-palatal, large oblong columellar-parietal, and shallow curved basal and rectangular palatal embayment. Numerous apertural barriers: parietal, angular, columellar and upper and lower palatal lamellae well developed. All of these barriers are spinosed and located deep inside the aperture, except the stout and elongate angular lamella is extended to the reflection of the peristome. Angular and parietal lamellae are elongated, located close to each other and nearly merge deep within the aperture, where the parietal lamella are seated lower than the angular lamella. Upper and lower palatal lamellae are well developed; two small interpalatal plicae: upper plica very small and lower plica large and prominent; two small infrapalatal plicae: upper plica large and more prominent than lower plica; two small and weak infraparietal plicae present in curvature between parietal and columellar lamellae (Figs. 2.3E, 2.4D). Umbilicus widely opened.

Derivation of name

The specific epithet *plesiolopa* is derived from the Greek words "*plesios*", meaning "near", and "*lopas*", meaning "plate", and refers to the fact that the angular and parietal teeth are in close connection.

Distribution and habitat

This new species, *Gyliotrachela plesiolopa* n. sp., seems to be restricted to Houaphane Province, close to North Vietnam. The specimens were collected from a humid limestone wall, surrounded by anthropogenic settlements and dense fruit orchards (Fig. 2.1).

Comparisons

This new species differs from *G. crossei* (Morlet, 1886) from North Vietnam by its smaller shell and presence of four whorls, while *G. crossei* has a larger shell (shell height about 3 mm) with five whorls. *Gyliotrachela plesiolopa* n. sp. differs from *G. saraburiensis* Panha and Burch, 2002 and *G. muangon* Panha and Burch, 2004 by having very closely located angular and parietal lamellae, a larger shell and perforated protoconch. *Gyliotrachela muangon* and *G. saraburiensis* can be clearly separated by the angular and parietal lamellae, while *G. muangon* has a smaller shell. *Gyliotrachela khaochongensis* Panha, 1997 has a larger shell size, last whorl is more ascending, and the peristome is continuous, thickened, expanded and with longer trumpet tuba (see Table 2.2).

Angustopila Jochum, Slapnik & Páll-Gergely, 2014

Angustopila Jochum et al., 2014: 26, 27.

Type species. *Systenostoma tamlod* Panha and Burch, 1999, by original designation.

Remarks

This genus is comprised of tiny vertiginid snails with a conical shaped shell, reticulated protoconch, aperture slightly closed or adnated to the last whorl and with or without apertural lamella (Panha and Burch, 1999b; Jochum et al., 2014).

Angustopila is distinguished from *Tonkinospira* Jochum et al., 2014 (= preoccupied name *Systenostoma* Bavay a Dautzenberg, 1908) by having a tiny shell (shell height ~1 mm) usually with apertural lamella, while *Tonkinospira* have larger shells (shell height 1–2.5 mm) and a lack of apertural lamella.

In addition, *Angustopila* is distinguished from *Krobylos* Panha and Burch, 1999 and *Montapiculus* Panha and Burch, 1999 by having a smaller shell (height usually < 1 mm), with a rounded whorl, apertural dentition varies from absent to containing parietal lamella and palatal plicae. In comparison, *Krobylos* has a larger shell (height 1.5–2.3 mm) with an angular whorl and no apertural dentition, and *Montapiculus* has a very wide and deep umbilicus, descending tuba and one palatal plica (Panha and Burch, 1999c) (Table 2.4).

Angustopila currently comprises of nine species; five species (*A. dominikae*, *A. fabella*, *A. huoyani*, *A. subelevata* and *A. szekeresi*) from China, three species (*A. concava*, *A. elevata* and *A. tamlod*) from Thailand and one species (*A. neglecta*) from peninsular Malaysia. All of these species are restricted to limestone areas and three of them (*A. neglecta*, *A. huoyani* and *A. tamlod*) have only been discovered only in caves.

Angustopila singuladentis **Inkhavilay & Panha n. sp.**

Figures 2.1, 2.5A–C, Tables 2.1, 2.2, 2.4

Type specimens. Holotype CUMZ 7063 (H = 1.1 mm, W = 0.9 mm; Figs. 2.5A–C).

Paratype CUMZ 7064 (49 specimens in ethanol), NHMUK (2 shells), SMF (2 shells).

Type locality. Xang Lod Cave, Viengxay District, Houaphane Province, Laos (20° 24' 31.3" N, 104° 13' 19.7" E), 882 m amsl.

Diagnosis

Angustopila singuladentis n. sp. has a conical shell, rounded whorls and shell sculptured with irregular growth line crossed with fine spiral striae. Protoconch is

perforated. Aperture simple, peristome slightly expanded with a strong parietal lamella.

Description

Shell minute, conical, white and transparent, about 3½ whorls, rounded, spire conical, suture depressed and blunt apex, shell height 0.7–1.0 mm and width 0.6–0.9 mm (Fig. 2.5A). Embryonic shell about 1½ whorls, nearly smooth with perforated sculpture (Fig. 2.5C). Teleoconch with irregular growth lines crossed with fine spiral threads. Last whorl shouldered. Aperture circular, open vertically, peristome continuous, lip slightly thickened and slightly expanded. Parietal callus thickened and slightly elevated from the last whorl. Apertural barrier well developed, thickened with strong parietal lamella (Fig. 2.5B). Umbilicus narrow and deep.

Derivation of name

The specific epithet *singuladentis* is derived from the Latin words "*singulus*", meaning "one", and "*dentis*", meaning "tooth", and refers to the single parietal lamella.

Distribution and habitat

The new species, *Angustopila singuladentis* n. sp., is currently known only from the type locality. The specimens were collected on the wet stalactites and on the cave walls at about 100 to 200 m inside from the cave entrance. However, the Xang Lod Cave (= pass through by the elephant) has become a famous tourist attraction site, the activities of which may impact negatively upon the population of these endemic cave dwelling snails (Fig. 2.1).

Comparisons

This new species closely resembles *A. tamlod*, but is distinct in having only one parietal lamella and three whorls, while *A. tamlod* has one parietal lamella and a small palatal plica with four whorls. *Angustopila singuladentis* n. sp. differs from *A. huoyani* Jochum et al., 2014 in having a smaller shell, three rounded whorls with thin spiral striae and one parietal lamella, whereas *A. huoyani* has a larger shell, five shouldered whorls with reticulated granules, and with one parietal lamella and one palatal plica.

This new species can be distinguished from *A. elevata* (Thompson and Upatham, 1997) and *A. concava* (Thompson and Upatham, 1997) by having three whorls, a rounded aperture, peristome adnated to the preceding whorl and a strong parietal lamella. In comparison, *A. concava* has 5–6 whorls, a wide umbilicus and curved parietal wall, while *A. elevata* has four whorls, peristome free from the preceding whorl and lamella absent (Table 2.1).

Family DIAPHERIDAE Panha & Naggs, 2010

Genus *Sinoennea* Kobelt, 1904

Ennea (*Sinoennea*) Kobelt, 1904: 26, 30.

Sinoennea—Zilch, 1960: 573. Richardson, 1988: 154. Benthem Jutting, 1961: 8, 9. Schileyko, 2000: 800.

Type species. *Pupa strophiodes* Gredler, 1881, by original designation.

Remarks

The genus *Sinoennea* is characterized by having a pupa- to long cylindrical-shaped shell with strong axial ridges to a smooth surface and a wide to narrow

umbilicus. Aperture rounded to oval shaped, apertural barriers normally contain parietal, columellar and basal lamellae with small palatal lamella sometimes present (Kobelt, 1904; Zilch, 1959-1960; Benthem Jutting, 1961; Schileyko, 2000).

The genus is comprised of about 55 nominal species (Richardson, 1988), and two newly described species were recorded from Thailand (Panha and Burch, 2005). Over ten species have been recorded from Indochina areas, including South China (Yen, 1939; Panha and Burch, 2005; Schileyko, 2011).

***Sinoennea lizae* Maassen, 2008**

Figures 2.1, 2.6A–C, Tables 2.1, 2.3

Sinoennea lizae Maassen, 2008: 235, figs 1-4. Type locality: 500 m SE of Phou Lek Village,
Oung Pra Ngiene, Vieng Phouka, Luang Namtha, Laos.

Material examined

Vieng Sawang Village, Vieng Phouka District, Luang Namtha Province, Laos (20° 41' 14.9" N, 101° 4' 8" E), and 687 m amsl: CUMZ 7065 (1 shell, Fig. 2.6A); CUMZ 7066 (7 shells).

Remarks

Sinoennea lizae differs from *S. macrodonta* (Bavay and Dautzenberg, 1912) and *S. hippocrepis* (Bavay and Dautzenberg, 1912) from North Vietnam in having a larger shell (height about 4–5 mm), nine whorls, ovate aperture, and the parietal callus extended about two-thirds of the last whorl. *Sinoennea macrodonta* has a smaller shell (height about 3 mm), six whorls, subcircular aperture and bifurcated palatal

lamella, and *S. hippocrepis* has a larger shell (height 8 mm), ten whorls, rounded peristome and a weaker palatal plica (Table 2.3).

Sinoennea lizae is only known from Luang Namtha, Northern Laos. All shells were collected from the ground among the thick leaf litter at a limestone outcrop base (Fig. 2.1).

***Sinoennea euryomphala* Inkhavilay & Panha n. sp.**

Figures 2.1, 2.6D–F, Tables 2.1, 2.3

Type specimens. Holotype CUMZ 7067 (H = 5.1, W = 2.2; Figs. 2.6D–F).

Paratypes CUMZ 7068 (3 shells), NHMUK (1 shells), SMF (1 shells).

Type locality. Pathok Cave, Ngoi District, Luang Phrabang Province, Laos (20° 33' 17.6" N, 102° 37' 47.0" E), 330 m amsl.

Diagnosis

Sinoennea euryomphala n. sp. has well developed transversed ribs (35 ribs on the last whorl); embryonic shell smooth. Aperture is ovate and free from the last whorl. Apertural barriers consist of a thick, strong curved angular lamella; upper and lower palatal lamellae are almost separated. Umbilicus is opened widely.

Description

Shell is pupa shaped, much inflated compared to *S. lizae*, and white and transparent with 8–9 whorls. Preceding whorls gradually increasing in size to largest last whorl before transforming to tuba and aperture. Shell height 4.7–5.3 mm and width 2.0–2.1 mm (Fig. 2.6D). Apex obtuse; embryonic shell about 2¾ whorls, smooth surface (Fig. 2.6F), and subsequent whorls with strong radial ridges of about 35 ridges on last whorl. Last whorl flattened; other whorls moderately rounded; suture

depressed and wide. Aperture narrow, subcircular shaped, opened vertically. Peristome continuous, broad and free from last whorl; lip thickened, expanded and slightly reflected. Parietal-angular lamella large, strong, crest-like shape and slightly curved entering the aperture. Palatal plica bifurcated and reaches to the apertural margin. Columellar long, high fold vertically located in the interior of the aperture (Fig. 2.6E). Umbilicus widely opened and deep.

Derivation of name

The specific name "*euryomphala*" is derived from the Greek words "*eurys*", meaning "broad or wide", and "*omphalos*", meaning "navel, and refers to the widely opened umbilicus, which is the prominent character of this species.

Distribution and habitat

Sinoennea euryomphala n. sp. is known only from the type locality. The specimens were collected on the ground under thick leaf litter and some specimens were found in the rock crevices of a limestone wall outside the cave (Fig. 2.1). The evergreen forest vegetation was dense with mosses on limestone walls.

Comparisons

Sinoennea euryomphala n. sp. differs from *S. macrodonta* and *S. hippocrepis* in having nine whorls, a widely opened umbilicus and the peristome is free from the last whorl. In comparison, the two latter species have a narrow to rimate umbilicus and the peristome adnated to the last whorl. In addition, *S. macrodonta* has a smaller shell with six whorls, while *S. hippocrepis* has a larger shell, 10 whorls and a rounded peristome (Table 2.3).

This new species can be distinguished from *S. calva* (Dautzenberg, 1893) and *S. atomaria* (Dautzenberg, 1893) in having a widely opened umbilicus and a peristome

free from the penultimate whorl. In contrast, the latter two species have a peristome adnated to the last whorl and a very narrow umbilicus. In addition, *S. calva* has a smaller shell, aperture sub-circular, suture impressed, and six whorls. *Sinoennea calva* has a strong columella, firmly located inside the aperture, while *S. atomaria* has a very small shell size with five whorls.

Sinoennea euryomphala n. sp. differs from *S. prima* Panha and Burch, 1999 and *S. lizae* in its widely opened umbilicus and peristome free from the last whorl. In comparison, *S. prima* has 27 radial ribs on the last whorl, the peristome is rounded, thickened and expanded, with very strong parietal and two palatal barriers nearly equal in size, while *S. lizae* has a smaller shell size that is cylindrical shaped, white, glossy and transparent, the aperture is adnated about 3/4 of the penultimate whorl, parietal lamella project downwards in close connection to the upper palatal lamella making a small parieto-palatal slit, the large columellar lamellae are seated deeper inside (Table 2.3).

Discussoin

This paper is the first revision of the micro pulmonated snails in Laos since the first species, *Paraboysidia wangviengensis* Panha and Tongkerd, 2002, was described. The two limestone faunistic surveys in Laos from 2013 to 2014 showed that the malacolfauna were not diverse even in limestone areas. Some larger snails such as ariophantids, camaenids, plectopylids, streptaxids and subulinids have been discovered, but these were less diverse compared to the records from the same latitude in Thailand and Vietnam or at a different latitude in Malaysia (Benthem Jutting, 1949; Panha and Burch, 2005; Schileyko, 2011). The apparently low species diversity in Laos may, however, reflect the surveys in Laos had less sampling sites and also examined fewer caves, while the sampling period during September 2013-December 2014 was quite dry with an average rainfall from 180 mm in September gradually

decreasing to 10 mm in December (The National Hydrological and Meteorological Services, 2014). Therefore, repeat samplings are still needed to confirm whether northern Laos is less diverse for terrestrial snails.

Paraboysidia anguloobtusus n. sp. and *P. paralella* n. sp. were collected from almost the same locality as *P. gittenbergeri* Maassen, 2008, in Luang Namtha province. However, they were proved to be separate species because of the quite unique apertural barriers compared to the several described species from nearby areas such as *P. lamothei* (Bavay and Dautzenberg, 1912), *P. nabhitabhatai* Panha and Burch, 2002, *P. pangmapaensis* Panha and Burch, 2001, *P. paviei* (Bavay and Dautzenberg, 1912) and *P. wangviangensis* Panha and Tongkerd, 2002. The great angular dentitions are prominent for both new species although the palatal and parietal lamellae arrangements and size are quite varied (Figs. 2.2, 2.3 and 2.4).

Gyliotrachela plesiolopa n. sp. is the first species of the genus recorded in Laos and has similar shell characters to the other described species, with a close location between the angular and parietal lamellae and an approximately medium sized shell compared with the other described species. The genus *Gyliotrachela* seems to be very conservative in showing almost identical shell characters and their trumpet shaped last whorls is an easily observed characteristic when attached to limestone walls.

Angustopila singuladentis n. sp. is also the first species of this genus recorded in Laos, and is a tiny cave dwelling species living mostly on wet stalactite structures. The three whorls and one parietal lamella are the dominant characters. It seems that the new species has the lowest number of whorls (three) compared with other described species in this genus that have 4–6 whorls.

Sinoennea euryomphala n. sp. is the second diapherid species ever recorded in Laos, with *S. lizae* Maassen, 2008 being the first one. Both species are found in the north of Laos. *Sinoennea lizae* has a cylindrical-shaped shell, while the new species has a pupa shaped or inflation shell character. The close connection of the parietal

lamella and upper palatal lamellae the makes an embayment in *S. lizae* but becomings a parieto-palatal slit in *S. euryomphala* n. sp. are the diagnostic separating characters.

The identification of micro terrestrial snails by their shells is still a standard method for the family Vertiginidae, which has been found to be informative with a strong discriminatory power in many genera such as *Boysidia*, *Paraboysidia* and *Hyselostoma*, but is controversial in many other genera such as *Acinolaemus*, *Anauchen* and *Gyliotrachela* (Thompson and Upatham, 1997; Panha and Burch, 2005). Systematic analysis using DNA sequencing has been employed and proved to support the shell identification in many genera (Tongkerd et al., 2004; Schilthuizen et al., 1999; 2004). However, further molecular analyses at both the species and population levels are needed for making a standard classification of terrestrial micro pulmonate snails.

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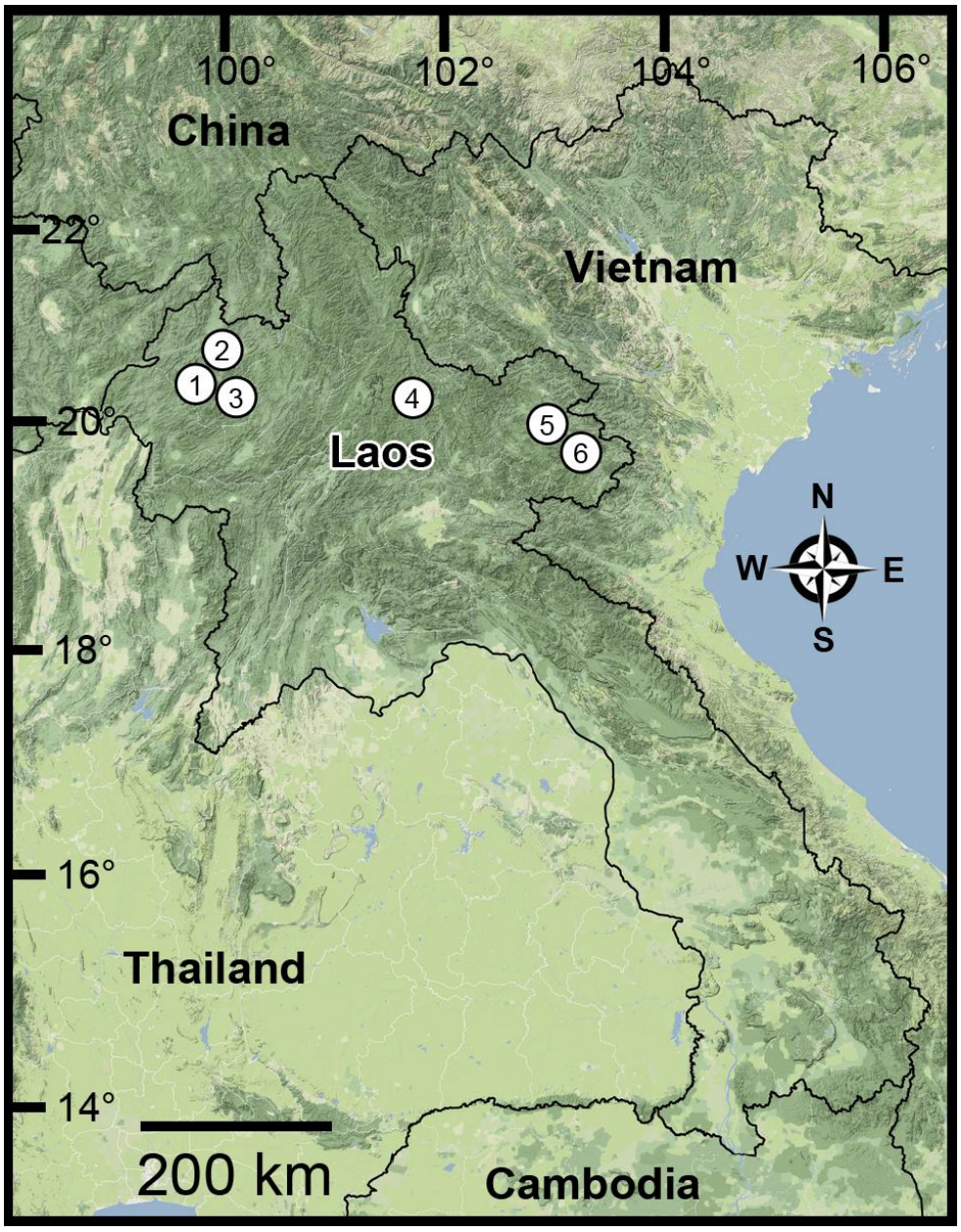

Figure 2.1 Map of Laos showing the approximate locations of the sampling sites and the type localities: (**1**) Sampling sites of *Paraboysidia gittenbergeri* and *Sinoennea lizae* from Luang Namtha; (**2**), Type localities of *Paraboysidia anguloobtusus* n sp.; and *Paraboysidia paralella* n. sp.; (**3**), Type localities of *Paraboysidia gittenbergeri* and *Sinoennea lizae*; (**4**), Type locality of *Sinoennea euryomphala* n. sp.; (**5**), Type locality of *Angustopila singuladentis* n. sp.; (**6**), Type locality of *Gyliotrachela plesiolopa* n. sp

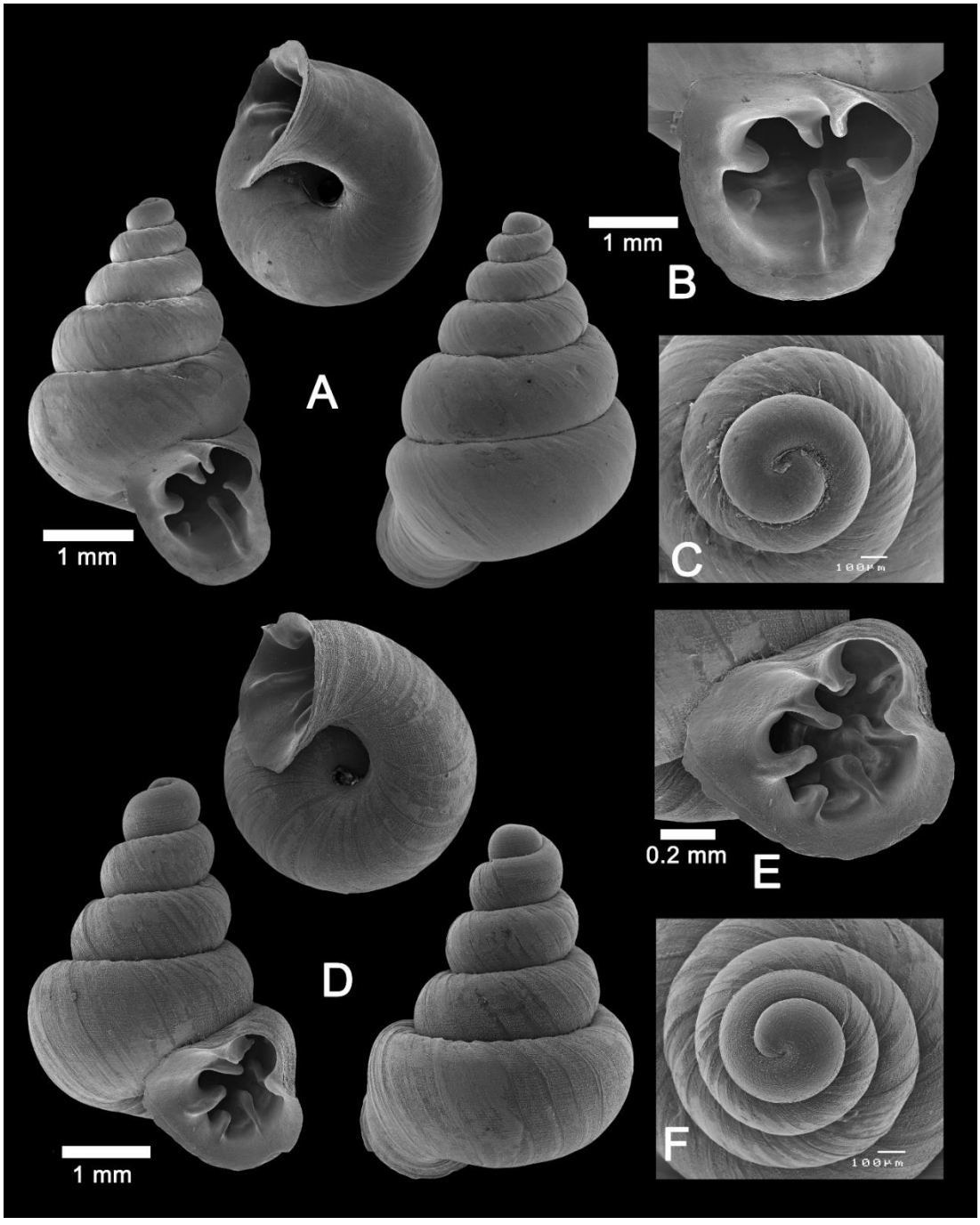

Figure 2.2 SEM images showing the shell shapes, apertural barriers and protoconch sculptures of (**A–C**), *Paraboysidia gittenbergeri* (CUMZ 7055) from Luang Namtha and (**D–F**), *Paraboysidia anguloobtusus* n. sp. (holotype CUMZ 7057).

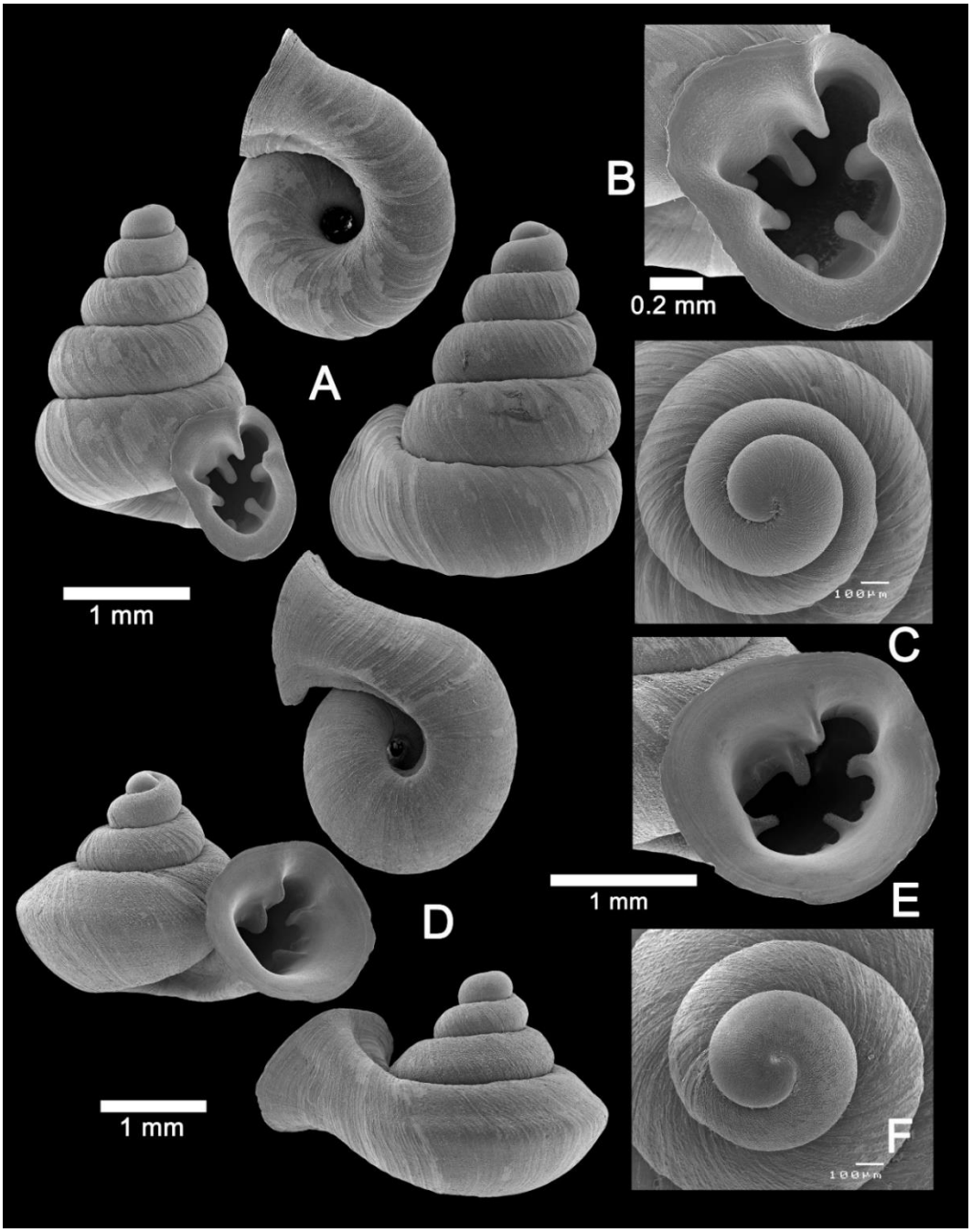

Figure 2.3 SEM images showing the shell shapes, apertural barriers and protoconch sculptures of (**A–C**) *Paraboysidia paralella* n. sp. (holotype CUMZ 7059) from Luang Namtha and (**D–F**) *Gyliotrachela plesiolopa* n. sp. (holotype CUMZ 7061) from Houaphane.

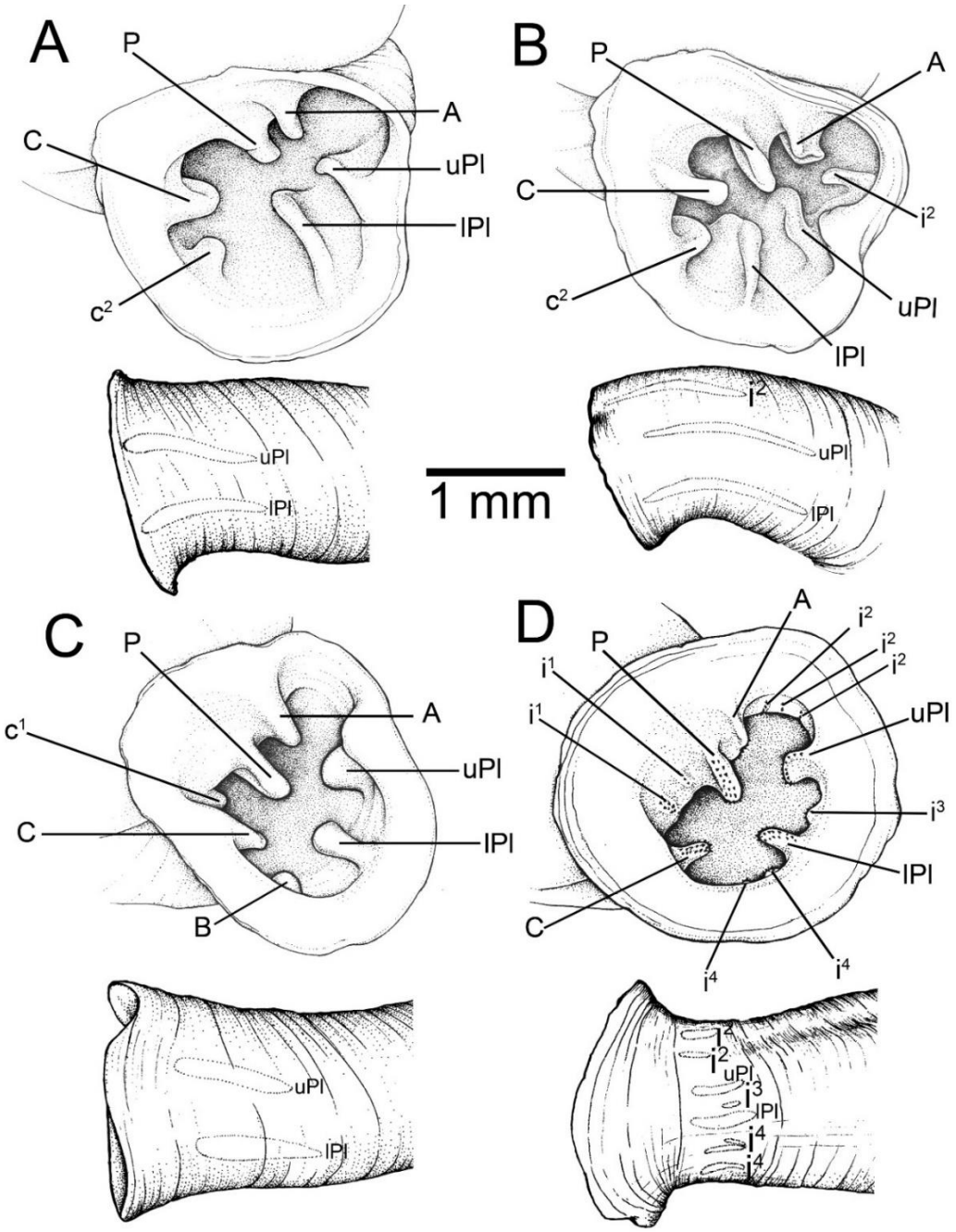

Figure 2.4 Illustrations of the shell apertural barriers showing the lamellae and plicae of (**A**) *Paraboysidia gittenbergeri*, (**B**) *Paraboysidia anguloobtusus* n. sp., (**C**) *Paraboysidia paralella* n. sp. and (**D**) *Gyliotrachela plesiolopa* n. sp.

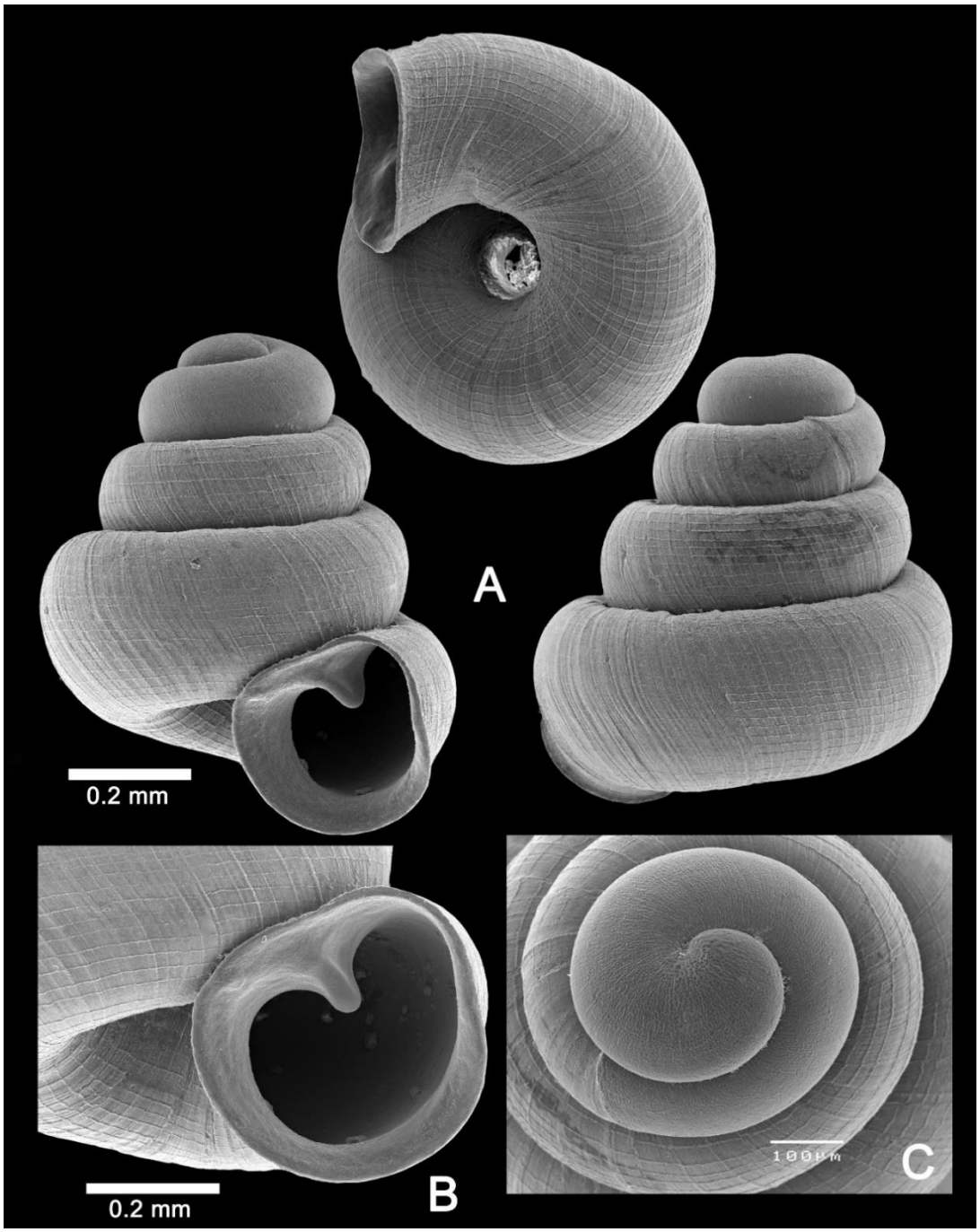

Figure 2.5 SEM images of shells showing the apertural barriers and protoconch sculpture of (**A–C**), *Angustopila singuladentis* n. sp. (holotype CUMZ 7063) from Houaphane.

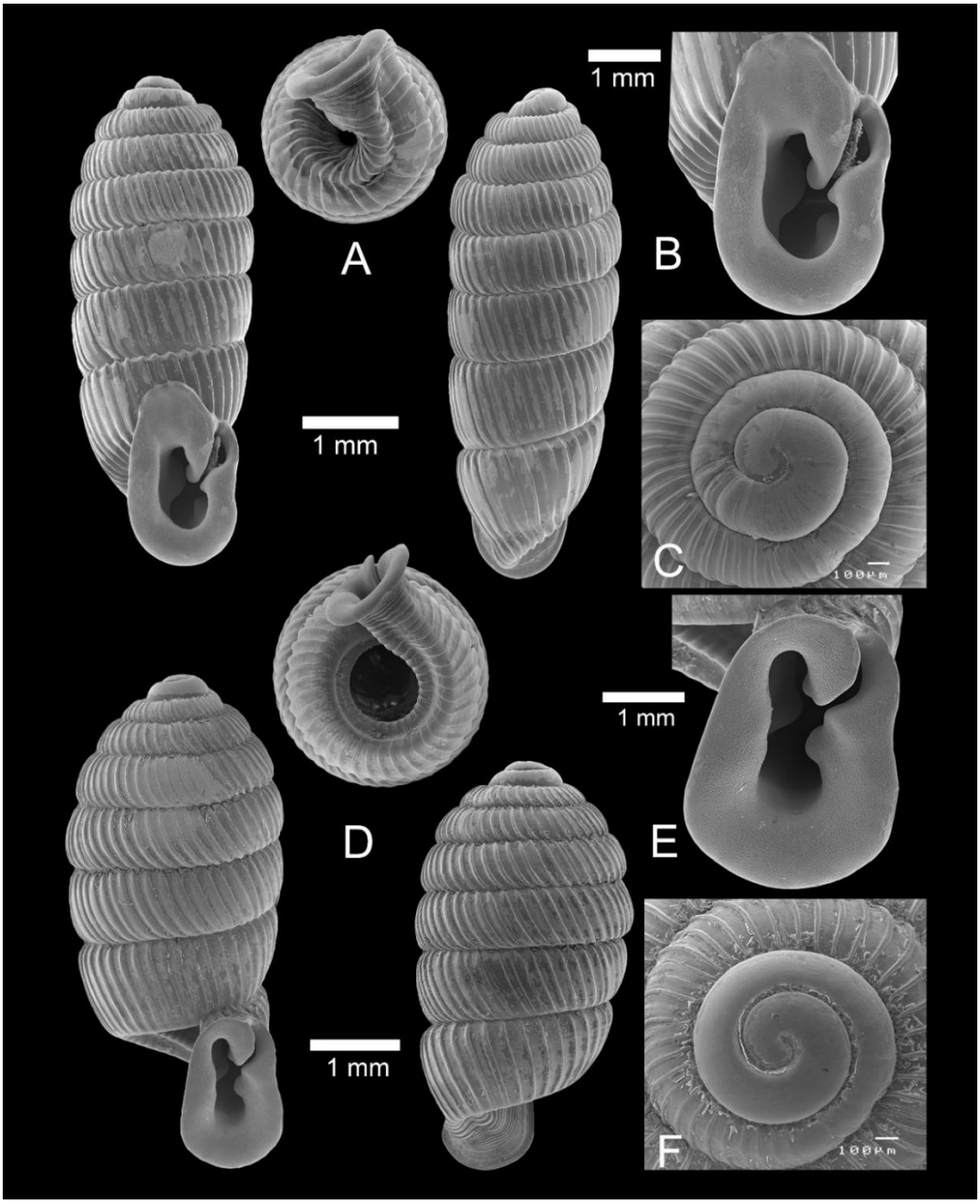

Figure 2.6 SEM images of shells showing the apertural barriers and protoconch sculptures of (**A–C**) *Sinoennea lizae* (CUMZ 7065) from Luang Namtha and (**D–F**) *Sinoennea euryomphala* n. sp. (holotype CUMZ 7067) from Luang Phrabang.

Table 2.1 Shell measurements and catalogue numbers (indicated in parentheses) of the seven examined species.

Species and CUMZ nos.	No. of specimens	Ranges, mean ± S.D. (mm)		
		H	W	H/W ratio
Paraboysidia gittenbergeri				
CUMZ 7055, 7056	17	4.1–5.2	2.5–3.0	1.4–1.9
		4.4 ± 0.26	2.7 ± 0.14	1.6 ± 0.10
Paraboysidia anguloobtusus n. sp.				
Holotype (7057)	9	1.8–2.1	1.4–1.6	1.2–1.3
paratypes (7058)		1.9 ± 0.11	1.5 ± 0.04	1.2 ± 0.05
Paraboysidia paralella n. sp.				
Holotype (7059),	43	2.3–2.9	1.6–2.2	1.1–1.7
paratypes (7060)		2.7 ± 0.16	1.8 ± 0.14	1.4 ± 0.13
Gyliotrachela plesiolopa n. sp.				
Holotype (7061),	29	1.5–2.2	2.6–3.4	0.4–0.7
paratypes (7062)		2.0 ± 0.16	3.2 ± 0.16	0.6 ± 0.05
Angustopila singuladentis n. sp.				
Holotype (7063),	50	0.7–1.0	0.6–0.9	0.9–1.2
paratypes (7064)		0.6 ± 0.06	0.8 ± 0.05	1.1 ± 0.06
Sinoennea lizae				
CUMZ 7067; 7066	7	4.2–4.9	1.7–1.9	2.2–2.7
		4.5 ± 0.22	1.8 ± 0.06	2.4 ± 0.15
Sinoennea euryomphala n. sp.				
Holotype (7067),	4	4.7–5.3	2.0–2.1	2.2–2.6
paratypes (7068)		5.0 ± 0.22	2.1 ± 0.06	2.4 ± 0.15

Table 2.2 Comparative shell morphology of the *Paraboysidia* spp., *Gyliotrachela* spp. and *Angustopila* spp.

Species	H x W (mm)	Whorls	Aperture shaped	Protocnch sculpture	Last whorl sculpture	Apertural barriers	Type locality	References
Paraboysidia								
P. paviei *	1.8 x 1.5	5	Subtriangular	?	Scarcely growth striae	i[1] present; long lPl.	Pac-Kha, Long-Ping, Vietnam	(Bavay and Dautzenberg, 1912)
P. lamothei *	3 x 2	5	Ssubquadrate	?	Inconspicuous growth-striae	A downward and meet uPl; i[1] present	Muong-Kong, Vietnam	(Bavay and Dautzenberg, 1912)
P. robusta *	5 x 3.2	6	Subquadrate	Smooth	Irregular growth striae	A and P not separated; C oblique	Phong-Tho, Vietnam	(Bavay and Dautzenberg, 1912)
P. nabhitabhatai	1.7 x 1.3	4¾	Subcircular	?	Close-set, spiral striae	A with two cusps	Chaiyaphumi, Thailand	(Panha and Burch, 2001)
P. wangviangensis	1.2 x 1.0	4½	Ovate	?	Spiral growth	A largest and strong	Vang Vieng, Laos	(Panha and Tongkerd, 2002)
P. pangmapaensis	1.7 x 1.1	4½	subcircular	?	Spiral striae	P largest and twist	Mae Hongson, Thailand	(Panha and Burch, 2001)

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Table 2.2 Comparative shell morphology of the *Paraboysidia* spp., *Gyliotrachela* spp. and *Angustopila* spp. (Continued).

Species	H x W (mm)	Whorls	Aperture shaped	Protocnch sculpture	Last whorl sculpture	Apertural barriers	Type locality	References
P. gittenbergeri	4.1–5.8 x 2.5–3.0	5¾	Semi-rounded to ovate	Smooth	Irregular growth lines	A and P well separated	Luang Namtha, Laos	(Maassen, 2008)
P. anguloobtusus n. sp.	1.8–2.1 x 1.4–1.6	4¾	Heart-shaped	Carina spiral or striae	Fine spiral striae	A with curved	Luang Namtha, Laos	
P. paralella n. sp.	2.3–2.9 x 1.6–2.2	4¾	Oval to semi-circular	Spongy-like	Irregular growth lines	B present	Luang Namtha, Laos	
Gyliotrachela								
G. crossei *	3 x 4.5	5	Subtriangle	?	Irregular growth line or striae	c^1 and B present	Tonkin	(Morlet, 1886)
G. khaochongensis	2.2 x 2.9	4	Rounded	Smooth	Irregular growth lines	c^1 present; one i^1; two i^3	Trang, Thailand	(Panha, 1997)
G. saraburiensis	2.2 x 2.9	4 ¾	Almost rounded, and upward about 17°	Pitted, spiral striae	Spiral striae	Three i^1;i^3; five i^4.	Saraburi, Thailand	(Panha and Burch, 2002)
G. muangon	1.8 x 1.3	4 ¾	Almost rounded	Spiral sulcus	Radial ribs	A and P well separated; c^2 absent	Chiangmai, Thailand	(Panha and Burch, 2004)

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Table 2.2 Comparative shell morphology of the *Paraboysidia* spp., *Gyliotrachela* spp. and *Angustopila* spp. (Continued)

Species	H x W (mm)	Whorls	Aperture shaped	Protocnch sculpture	Last whorl sculpture	Apertural barriers	Type locality	References
G. plesiolopa n. sp.	1.5–2.2 x 2.6–3.4	4	Almost rounded, and upward about 20°	Distinct spongy-like	Irregular growth line or striae	**A** and **P** closed; two i^1; one i^3; two i^4	Huaphan, Laos	
Angustopila								
A. concava *	1.0–1.2	4.6-5.3	Kidney-shaped	Reticulating granules	Spiral threads more apparent	Weak **P**	Nakhon Ratchasima, Thailand	(Thompson and Upatham, 1997)
A. elevata *	0.9 x 0.8	4	Ovate	Low granules	Fine raised spiral treads	**P** and **Pl** absent	Chiangmai, Thailand	(Thompson and Upatham, 1997)
A. tamlod	1.0 x 0.8	4¾	Semicircular to oval	?	Spiral threads	**P** and **Pl**	Mae Hong Son, Thailand	(Panha and Burch, 1999)
A. huoyani *	1.1 x 0.9	5	Semi-circular, oblique	Reticulating granules	Very fine irregular axial lamellae and reticulating microgranules	**P** and **Pl**	Hunan, Huoyan, China	(Slapnik and Páll Gergely, 2014)
A. singuladentis n. sp.	0.7–1.0 x 0.6–0.9	4½	Almost circular	Spongy-like	Fine raise spiral crossed by irregular growth line	Only **P**	Houaphane, Laos	

? =Character not mentioned in the literature. * = Information was taken from the original descriptions.

[1] = Characters in bold indicate the apertural barrier type, with the abbreviations as mentioned in the Materials and Methods.

Table 2.3 Comparative shell morphological characters among the *Sinoennea* species.

Species	Height	Whorls	Aperture shaped	Apertural barriers[1]	Protoconch sculpture	Type locality	References
S. larvula *	3.45	6	Quadrangular	**P**, **C** and weak **Pl**	?	Ning-Kuo-fu Anhwei, China	(Heude, 1882)
S. fuchsi *	5-5.5	8	Ovate-triangular	**P**, **C** and **Pl**	Carina striae	Kwei-dshou, China	(Gredler, 1885)
S. calva *	4	6	Subcircular	**P**, **C**, **Pl** and **B**	Smooth	Haiphong, Vietnam	(Dautzenberg, 1893)
S. atomaria *	2.5	5	Quadrangula?	**P**, **C**, **Pl** and **B**	Smooth	Haiphong, Vietnam	(Dautzenberg, 1893)
S. hippocrepis *	8	10	Subbcircular	**P**, **C** and **Pl**	Smooth	Phong-Tho, Tonkin	(Bavay and Dautzenberg, 1912)
S. macrodonta *	3	6½	Subtriangcle	**P**, **C** and bifid **Pl**	?	Muong Kong, Tonkin	(Bavay and Dautzenberg, 1912)
S kwangsiensis *	3.5	7	Rounded	**P**, **C** and two **Pl**	Smooth	Kwangsi, China	(Yen, 1939)
S. prima	4.9	8½	Quadrangular-ovate	**P**, **C** and two **Pl**	Smooth	Chiangmai, Thailand	(Panha and Burch, 1999)
S. ranongensis	2.7	5¾	Subtriangle to heart-shape	**P**, **C** and two **Pl**	Fine striae	Ranong, Thailand	(Maassen, 2008)
S. lizae	3.4–3.6	8 ½	Long-oval	**P**, **C** and spaced **Pl**	Smooth	Luang Namtha, Laos	
S. euryomphala n. sp.	4.7–5.3	9	Subcircular	**P**, **C** and **Pl**	sSmooth	Luang Phrabang, Laos	

? =Character not mentioned in the literature. * = Information was taken from the original descriptions.

[1] = Characters in bold indicate the apertural barrier type, with the abbreviations as mentioned in the Materials and Methods.

Table 2.4 Comparative shell morphological characters among the four genera: *Krobylos* Panha and Burch, 1999, *Montapiculus* Panha and Burch, 1999, *Tonkinospira* Jochum et al., 2014 and *Angustopila* Jochum et al., 2014.

Characters	*Krobylos**	*Montapiculus**	*Tonkinospira**	*Angustopila**
Type species	*K. pomjuk* Panha and Burch, 1999	*M. proboscidea* Panha and Burch, 1999	*Systenostoma pauperrima* Bavay and Dautzenberg, 1908	*Systenostoma tamlod* Panha and Burch, 1999
Shell shape	Helicoid, with a depressed to elongate spire	Mountain-shaped, raise spire	Conical or depressed conical	Conical
Shell height (mm)	1.4-2.3	1.6	1-2.5	0.9-1.2
Shell width (mm)	1.2-2.1	1.55	1 6-2.5	0.80-1.1
Whorl numbers	3-5	5	4-5	4-5
Aperture	Ovate to semi-circular and adnate to last whorl	D-shape with descending tuba	Oblique and adnate to Last whorl	Ovate, oblique or semi-circular and free from last whorl
Apertural barriers	Absent	Parietal and palatal	Absent	One or two barriers
Protoconch sculpture	Smooth	Smooth	Spiral line	Smooth
Last whorl	Ddescending	Directed downward	Descending	Descending
Last whorl sculpture	Without spiral striae	With spiral striae	Without spiral striae	Without spiral striae
Umbilicus	Narrow	Very wide and deep	Narrow to wide	Narrow
Distribution	Northern Thailand and Laos	Central Thailand	Northern Vietnam	Northern Thailand and South of China

? =Character not mentioned in the literature. * = Information was taken from the original descriptions.

Chapter III

The first revision of carnivorous land snail family Streptaxidae in Laos, with description of three new species (Pulmonata, Stylommatophora, Streptaxidae)

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Abstract

The family Streptaxidae in Laos is revised. Twelve species are known, mainly from limestone areas, in the genera *Discartemon* Pfeiffer, 1856, *Perrottetia* Kobelt, 1905, *Haploptychius* Möllendorff, 1906, and *Indoartemon* Forcart, 1946. Three new species, *P. unidentata* **sp. n.** and *P. megadentata* **sp. n.** from northern and central Laos, and *I. diodonta* **sp. n.** from central Laos, are described. All eight species of these three genera previously recorded from Laos are revised and discussed based on examined material from Laos, Cambodia, Vietnam and Thailand. Type material was examined and lectotypes are designated. Details of genital anatomy and radulae are provided, including the first detailed genitalia and radula descriptions from *Haploptychius*. Two novelties in Streptaxidae, a vaginal caecum, and the occurrence of aphallic individuals, are reported from *H. pellucens* (Pfeiffer, 1863).

Keywords

Limestone, tropical forest, systematics, type specimen, Southeast Asia, predator, taxonomy, aphally.

Introduction

The Streptaxoidea currently comprises two families, the worldwide Streptaxidae Gray, 1860 and the Southeast Asian endemic Diapheridae Panha and Naggs, 2010 (Richardson, 1988; Rowson et al., 2010a; Schileyko, 2000; Sutcharit et al., 2010b). The Streptaxidae Gray, 1860 are active predators with an eccentric to cylindrical shell, usually with apertural dentition, and a yellowish to orange soft body (Rowson et al., 2010b; Schileyko, 2000; Siriboon et al., 2013; Siriboon et al., 2014a; Siriboon et al., 2014b; Zilch, 1960).

Early classifications of the family such as (Kobelt, 1905–1906), used mainly shell shape and the arrangement of apertural dentition. However, many shell characters are highly conserved or occur recurrently, making some species and genera difficult to separate. Fortunately, the reproductive organs of streptaxids can also be taxonomically significant (Rowson and Tattersfield, 2013 ; Schileyko, 2000; Siriboon et al., 2013; Siriboon et al., 2014a; Siriboon et al., 2014b). Few reports have contributed data on the genitalia of Southeast Asian taxa (Berry, 1963 ; Berry, 1965; Stoliczka, 1871) until recently (Páll-Gergely et al., 2015; Siriboon et al., 2013; Siriboon et al., 2014a; Siriboon et al., 2014b).

In Indochina, streptaxid diversity was throught to comprise only 10 genera and about 40 species (Bruggen, 1967). However, in the last decade 21 new species (more than half the previous total) and one new genus have been described from Indochina (Do and Do, 2015; Siriboon et al., 2013; Siriboon et al., 2014a; Siriboon et al., 2014b). Thirty-seven species are recorded from Thailand (Hemmen and Hemmen, 2001 ; Panha, 1996; Siriboon et al., 2013; Siriboon et al., 2014a; Siriboon et al., 2014b), 10 from Myanmar (Blanford and Godwin-Austen, 1908), and 45 from Vietnam (Schileyko, 2011). In contrast, only three species were reported from Laos in the past two centuries (Möllendorff, 1898; Pfeiffer, 1863a), with three others added in recent years (Do and Do, 2015; Schileyko, 2011).

Almost all groups of the land snail fauna in Laos have been less-well studied than those of neighbouring areas. The Lao People's Democratic Republic, until recently encompassed some of the most significant forest areas remaining in Southeast Asia such as mountainous areas in the north and limestone karsts in central area, and some of the most intact biota left in Asia (Kemp, 2011). Those habitat characteristics also harbor diverse of terrestrial molluscan fauna. The present paper focuses on the four genera, *Discartemon* Pfeiffer, 1856, *Perrottetia* Kobelt, 1905, *Haploptychius* Möllendorff, 1906, and *Indoartemon* Forcart, 1946 that were formerly recorded from

Laos. Genital anatomy and shell micro-structures of are carefully investigated. The type specimens of all known species were examined, and the penial hooks and radula morphology of *Haploptychius* are defined for the first time. This adds significantly to knowledge of the Streptaxidae in Indochina and especially in Laos.

Materials and Methods

Animals were collected from evergreen forest in the north, and limestone karsts and dipterocarp forest in the south of Laos. Live specimens were photographed and then stored at -20 ℃ and then preserved in 70% ethanol (v/v) for anatomical studies. The identifications were based on Bavay and Dautzenberg (1903, 1908); Blanford and Godwin-Austen (1908); Kobelt (1905, 1906); Möllendorff (1898); Pfeiffer (1863) and Siriboon et al., (2013, 2014b). Shell height (H), shell width (W), whorl count and H/W ratio were measured and interpreted following Siriboon et al., (2013). Shells and genitalia were investigated and digital images taken using Cell'D Imaging Software. All live adult specimens of each species were dissected and the genitalia examined under a stereo-microscope and representatives selected for illustrations under a camera lucida. The buccal masses were removed, and the radulae were soaked in 10% NaOH then cleaned in distilled water. Radula, penial hooks and vaginal hooks were examined and photographed under SEM (JEOL, JSM-5410 LV). In the descriptions, 'proximal' relates to the genital orifice, and 'distal' refers to the region furthest away from the genital orifice. The term 'vaginal caecum' is defined herein.

Anatomical abbreviations. ag, albumen gland; at, atrium; fo, free oviduct; gd, gametolytic duct; gs, gametolytic sac; hd, hermaphroditic duct; ov, oviduct; p, penis; pr, penial retractor muscle; ps, penial sheath; psr, penial sheath retractor muscle; sv, seminal vesicle; ta, talon; v, vagina; vc, vaginal caecum; vd, vas deferens (Siriboon et al., 2013, 2014a, b).

Institutional abbreviation

Materials examined in this study were deposited in the following institutions:

CUMZ: Chulalongkorn University Museum of Zoology, Bangkok.

MNHN: Muséum National d'Histoire Naturelle, Paris.

NHMUK: The Natural History Museum, London.

NUOL: National University of Laos, Vientiane.

SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main.

Systematics

Family Streptaxidae Gray, 1860

Genus *Discartemon* Pfeiffer, 1856

Discartemon Pfeiffer, 1856: 173. Siriboon et al., 2014a: 48, 49.

Odontartemon (Discartemon)——Kobelt 1905: 91, 96.

Type species. *Streptaxis discus* Pfeiffer, 1851, by subsequent designation by Ancey (1884: 399).

Remarks

The genus was recently revised. For complete illustrations, species descriptions and dichotomous key see Siriboon et al., (2014a).

***Discartemon discus* (Pfeiffer, 1853)**

Streptaxis discus Pfeiffer, 1853: 252. Type locality: Unknown.

Streptaxis (Discartemon) paradiscus Möllendorff, 1900: 117. Type locality: Phucson bei Touranne, Annam [Da Nang Province, Vietnam].

Discartemon discus——Siriboon et al., 2014a: 53-55, figs 4A-C, 11A-C, 22A.

Material examined

Lectotype of *Streptaxis discus* Pfeiffer, 1853 NHMUK 20130684. Lectotype of *Streptaxis paradiscus* Möllendorff, 1900 SMF 108534 and paralectotypes SMF 108535 (5 shells).

Remarks

Discartemon discus has been recently re-described from the shell, genitalia and radula, and type specimens were re-investigated and illustrated (see Siriboon et al., 2014a).

All previous records of this species were all from "Annam" (Siriboon et al., 2014a). This term is a historical political division during the colonial period, with an uncertain boundary. The distribution of *D. discus* (=*D. paradiscus*) in Laos was reported by Schileyko (2000: 784, 2011: 23). However, no specimens were found by the present study and the records from Laos remain to be confirmed.

Genus *Haploptychius* Möllendorff, 1906

Haploptychius Möllendorff in Kobelt 1906: 127. Zilch 1960: 562. Richardson 1988: 211. Schileyko 2000: 796, 797.

Odontartemon (*Haploptychius*)—Thiele 1931: 730. Forcart 1946: 215.

Oophana (*Haploptychius*)—Benthem Jutting 1954: 76, 95.

Type species. *Streptaxis sinensis* Gould, 1859: 424 by original designation.

Description

Shell depressed to very distorted, mostly white-hyaline or transparent. Shell surface smooth and glossy or with fine radial ridges. Embryonic shell smooth; following

whorls increasing regularly; penultimate whorls slightly to strongly extended beyond body whorl. Last whorl rounded and more or less deviated from the vertical axis. Umbilicus narrowly open and deep. Aperture sub-circular to semi-ovate. Peristome expanded and reflected. Apertural dentition always consisting of a single parietal lamella. Schileyko (2000) includes species with a "smooth" parietal wall, i.e. without a lamella in *Haploptychius*, but whether such taxa belong in this genus requires further investigation.

Live specimens exhibit a semi-transparent bright yellow body, sometimes with brownish spots; skin reticulated. Upper tentacles yellow to orange, long, with black eye-spot on tip; lower tentacles short. Brownish digestive gland and black kidney may be visible through transparent shell. Foot narrow, undivided and with short tail.

Genitalia with long and slender penis; penial sheath long, about a half to whole length of penis. Internal wall of penis with numerous long and slender penial hooks in longitudinal arrangement. Vas deferens passes under penial sheath before connecting apically to penis. Vagina and free oviduct short. Seminal vesicle present, convoluted and short. Vaginal hooks not found.

Remarks

Currently, the genus *Haploptychius* consists of about 40 nominal species distributed from India to Indochina, south of China and Greater Sunda Islands (Kobelt, 1905–1906; Richardson, 1988; Schileyko, 2000; Zilch, 1961). Fifteen species were reported from Indochina, of which only three species: *H. pellucens* (Pfeiffer, 1863), *H. porrectus* (Pfeiffer, 1863) and *H. fischeri* (Morlet, 1887) were recorded from Laos (see Kobelt 1906; Pfeiffer 1863; Schileyko 2011).

General shell morphology of *Haploptychius* is quite similar to *Oophana* Ancey, 1884 and *Indoartemon* Forcast, 1946. However, it differs in having only a parietal lamella; while *Oophana* usually has parietal, palatal, columellar and basal lamellae,

and *Indoartemon* always has parietal and basal lamellae. In addition, the genitalia of *Haploptychius* have a penial sheath extends about a half to entire the penis length, vas deferens passes through penial sheath, and long slender penial hooks. In *Oophana*, the vas deferens enter the penial sheath apically with very short vagina (Berry 1963, Schileyko 2000); and *Indoartemon*, the vas deferens attached (not pass through) the penial sheath with small and short penial hooks (Siriboon et al., 2013).

Carinartemis Siriboon and Panha, 2014 resembles *Haploptychius* in having only a parietal lamella. However, it differs from *Haploptychius* in its very sharp peripheral keel and having the last whorl more deviated from the vertical axis. In addition, the genitalia has thick or thin penial sheath, penial hook short and stout, and vaginal hooks present (Siriboon et al., 2014a).

The relatively large, distorted heliciform shell and dentition restricted to a parietal lamella clearly differentiate *Haploptychius* from *Discartemon* Pfeiffer, 1856 and *Perrottetia* Kobelt, 1905 (Schileyko 2000, Siriboon et al., 2013, 2014a, b).

Haploptychius pellucens (Pfeiffer, 1863)

Figs 3.1, 3.2A, 3.3A–C, 3.7A, B, 3.8A–D, 3.9A–F, 3.10G; Table 3.1

Streptaxis pellucens Pfeiffer 1863 [1862]: 273, pl. 36, fig. 6. Type locality: Lao Mountain, Camboja [Cambodia]. Martens 1867: 85. Pfeiffer 1868: 441. Pfeiffer 1871: 29, pl. 115, figs 11, 12. Morlet 1883: 105, pl. 4, fig. 2, 2a. Tryon 1885: 71, 72, pl. 14, figs 98-100. Gude 1903: 212.

Haploptychius pellucens—Kobelt 1906: 132, 133, pl. 61, figs 17–20. Richardson 1988: 217, 218. Schileyko 2011: 24, 25.

Material examined

This species was described from the H. Cuming collection. An illustration of the shell and one set of measurements were given in the original description. Three

specimens from the Cuming collection at NHMUK have Pfeiffer's handwritten label stating the species name and locality. In order to stabilize the name, an identical specimen matching with the illustration and measurements given in the original description is designated here as lectotype NHMUK 20160249.1 (Fig. 3.3A; H = 11.7, W = 11.2). The other two remaining shells from the same lot then became paralectotypes NHMUK 20160249.2 (2 shells; Fig. 3.3B; H = 11.1, W = 10.6 and H = 13.1, W = 13.4).

Cambodia: NHMUK MacAndrew coll. (4 shells). Ban Namone, Xayabouly, Laos (about 40 Km. from Ngeun district, Lao-Thai border to Xayabouly district): CUMZ 6264 (Fig. 3.3C; 8 shells), 6265 (4 specimens in ethanol). Tam Phatok, Ngoi, Luang Phrabang, Laos: CUMZ 6267 (7 shells). Ngoi, Luang Phrabang, Laos: CUMZ 6268 (7 shells). Nam Ork Roo, Nathong, Namor, Oudomxay, Laos: CUMZ 6269 (29 shells), 2670 (6 specimens in ethanol; Figs 3.3A, B, 3.8A, 3.9A–F, 3.10G). Ban Oudom, Pak Beng, Oudomxay, Laos: CUMZ 6271 (15 shells). Tam Kao Rao, Vieng Phoukha, Luang Namtha, Laos: CUMZ 2672 (2 shells). Tam Mung Korn, Khamkeurt, Bolikamxay, Laos: CUMZ 6266 (4 shells).

Description

Shell oblique-ovate, white and translucent. Whorls 6½, spire conical with distinct suture. Shell surface glossy with thin transverse ridges which diminish below periphery. Embryonic shell about 2½ whorls, with smooth surface; following whorls regularly coiled. Penultimate whorl and last whorl rounded, axially deflected. Aperture subcircular; peristome thin, little expanded and reflected. Apertural dentition with one more or less strong parietal lamella. Umbilicus open and deep (Fig. 3.3A–C).

Radula

Each row consists of 77-85 teeth with formula (38-42)-1-(38-42). Central tooth very small, triangular, with a pointed cusp. Lateral and marginal teeth undifferentiated,

lanceolate, unicuspid. Latero-marginal teeth gradually reduce in size, with outermost teeth much smaller and shorter than inner teeth (Fig. 3.10G).

Genital organs

Atrium (at) short. Proximal penis (p) stout about one-thirds of penis length; distal penis slender. Penial sheath (ps) thin, extending about half of penis length; penial sheath retractor muscle (psr) very thin, originating at atrium and inserted apically at penial sheath (Fig. 3. 6A). Vas deferens (vd) passes through about one-third of penial sheath length before entering into penis apically. Penial retractor muscle (pr) very thick and connected at penis apically (Fig. 3.7A, B).

Internal wall of atrium generally corrugated with numerous atrial pores (Fig. 3. 9A). Penial wall densely covered in light brown penial hooks, about 6 hooks/200 μm^2. Hooks located on low conical penial papillae, separated by thin reticulated folds. Penial hooks small (< 0.1 mm in length), long, slender, slightly expanded at base, tips pointed and curved towards genital orifice (Fig. 3.9B–E).

Vagina (v) short, about one-third of penis length. Gametolytic duct (gd) long tube extending to albumin gland; gametolytic sac (gs) ovate. Free oviduct (fo) proximally large with almost equal diameter to vagina, becoming narrower distally. Oviduct (ov) enlarged and folded; prostate gland inconspicuous and bound to oviduct. Talon (ta) small, short and club-shaped. Hermaphroditic duct (hd) bearing long and thin seminal vesicle. Seminal vesicle (sv) about three times longer than the length from talon to branching point of seminal vesicle (Fig. 3.7A).

Vaginal wall with series of transverse and undulated parallel vaginal folds; vaginal hooks absent (Fig. 3.9F).

Distribution

This species is known from several limestone areas from central to northern part of Laos. The animals can be found at altitudes from 150-300 meters above mean sea level.

Remarks

This species can be distinguished from *H. porrectus* by having a larger shell, more elevated spire elevated and less oblique aperture. The vas deferens passes through a shorter part of the penial sheath length, and the vagina wall has undulated transverse ridges rather than papillae. *Haploptychius pellucens* can be distinguished from *H. costulatus* (Möllendorff, 1881) from China by having a larger and thinner shell, narrower umbilicus and having the left periphery of the penultimate whorl extending beyond the diameter of the last whorl. *Haploptychius fischeri* differs from this species by having a larger, more depressed and thicker shell, with a more obtuse spire, and subquadrangular aperture (Fig. 3.3G).

All live adult specimens were dissected and the genitalia have been examined, and three different types of genitalia are observed. There are six fully adult specimens collected from Nam Ork Roo, Oudomxay with 'normal' genitalia (Fig. 3.8A). Two specimens from Ban Namone, Xayabouly have no male genital organs (penis, retractor muscle, vas deferens and prostate gland), while female genital organs are well developed and fully function (Fig. 3.8D). This is apparently the first report of aphallic animals in Streptaxidae. The other two specimens from Ban Namone have a 'normal' penis, but have an enlarged and curved "vaginal caecum (vc)" near the penis and atrium junction (Fig. 3.8B, C). This too is an unusual or unique structure in Streptaxidae. Nevertheless, all these animals appear conspecific based on their shells and the causes of this variation are unknown.

***Haploptychius porrectus* (Pfeiffer, 1863)**

Figs 3.1, 3.2B, 3.3D–F, 3.7C, D, 3.9G–M, 3.10H; Table 3.1

Streptaxis porrecta Pfeiffer 1863 [1862]: 273. Type locality: Lao Mountains, Camboja [Cambodia]. Martens 1867: 85. Pfeiffer 1868: 442. Tryon 1885: 74. Fischer 1891: 18. Gude 1903: 217. Gude, 1903: 275, 322, 325, pl. 12, figs 20–22.

Haploptychius porrectus—Kobelt 1906:133, pl. 61, figs 24-26. Richardson 1988: 219.

Material examined

This species was described from the H. Cuming collection. The number of specimens was not indicated, but only one set of measurements was given in the original description. The NHMUK collection contains two specimens from the Cuming collection that has Pfeiffer's handwritten label stating the species name and collection locality. In order to stabilize the name, a specimen matching with the measurements given in the original description is designated here as lectotype NHMUK 20140750.1 (Fig. 3.3D; H = 8.0, W = 9.0). The other specimen from the same lot becomes a paralectotype NHMUK 20140750.2 (Fig. 3.3E; H = 8.0, W = 8.2).

Laos: NHMUK 1906.1.1.770 (4 shells), NHMUK MacAndrew coll. (2 shells). Ban Nong Tang, Phou kood, Xieng Khuang, Laos: CUMZ 6273 (18 shells; Fig. 3.3F), 6274 (1 specimen in ethanol; Figs 3.2B. 3.7C, D). Tam Pew, Kham, Xieng Khuang, Laos: CUMZ 6275 (4 specimens in ethanol; Figs 3.9G–M, 3.10H).

Description

Shell oblique-heliciform, white and translucent. Whorls 6½, spire conical, suture distinct. Shell surface glossy, with transverse ridges that diminish below the periphery. Embryonic shell smooth with 2½ whorls; following whorls regularly coiled. Penultimate whorl rounded; last whorls rounded and axially deflected. Aperture

subcircular; peristome thickened and reflected. Aperture dentition with one parietal lamella. Umbilicus open and deep (Fig. 3.3D-F).

Radula

Each row consists of 46-58 teeth with formula (23-29)-1-(23-29). Central tooth very small and triangular, with a pointed cusp. Lateral and marginal teeth undifferentiated, lanceolate, unicuspid. Latero-marginal teeth gradually reduce in size, with outermost teeth much smaller and shorter than inner teeth (Fig. 3.10H).

Genital organs

Atrium (at) short. Proximal penis (p) stout about one-fifth of penis length; distal penis slender. Penial sheath (ps) thin, extending about two thirds of penis length; penial sheath retractor muscle (psr) very thin, originating at atrium and inserting distally on penial sheath (Fig. 3.7C). Vas deferens (vd) passes through about a quarter of the penial sheath length before entering into penis apically (Fig. 3.7D). Penial retractor muscle (pr) thick, short and connected with penis apically.

Internal wall of atrium generally smooth (Fig. 3.9G). Proximal penial wall densely covered with brownish penial hooks, about 10 hooks/200 μm^2. Hooks located on low conical penial papillae, separated by very thin reticulated folds. Proximal penial hooks small and short (< 0.04 mm in length), slightly expanded at base, tip sharp and directed towards genital orifice (Fig. 9H, I). Distal penial wall less densely scattered with brownish penial hooks, about 4 hooks/200 μm^2; penial papillae absent. Distal hooks very large, long and slender (< 0.5 mm in length), expanded at base, tip obtuse and directed towards genital orifice (Fig. 3.9J, K).

Vagina (v) short, about half of penis length. Gametolytic duct (gd) long tube extending as far as albumin gland; gametolytic sac (gs) small. Free oviduct (fo) short with almost the same diameter as vagina. Oviduct (ov) enlarged and folded; prostate

gland inconspicuous and bound to oviduct. Talon (ta) small and club shape. Hermaphroditic duct (hd) bearing very long and enlarged seminal vesicle (sv) about ten times longer than the length from talon to branching point of seminal vesicle (Fig. 3.7C).

Vaginal wall generally corrugated with irregular vaginal papillae (Fig. 3.9L, M). Vaginal hooks absent.

Distribution

This species is known from the limestone outcrops in northeastern and central part of Laos. The animals can be found at altitudes from 150-300 meters above mean sea level.

Remarks

This species can be distinguished from *H. dorri* (Dautzenberg, 1894) and *H. blaisei* (Dautzenberg and Fischer, 1905) in having a less depressed shell and less deviated last whorl. In addition, *H. blaisei* possesses a solid shell with an angular penultimate whorl, and *H. dorri* has a smaller and smooth shell with an angular penultimate whorl. *Haploptychius anceyi* (Mabille, 1887) is similar to *H. porrectus*, however, it differs in its smaller shell, circular aperture, and nearly smooth shell surface.

***Haploptychius fischeri* (Morlet, 1887)**

Fig. 3.3G

Streptaxis fischeri Morlet 1887 [1886]: 259, 274, pl. 12, fig. 1, 1a. Type locality: Baie d'Halong et Montagne de l'Éléphant [Elephant Mountain of Halong Bay, Quang Ninh Province, Vietnam]. Gude 1903: 212.

Haploptychius fischeri—Kobelt 1906: 136, pl. 61, fig. 21, Richardson 1988: 215. Schileyko 2011: 25.

Material examined

The species was described based on material from Jourdy's collection and an illustration was included in the original description (Morlet 1887: 259, pl. 12, fig. 1, 1a). There is a single specimen from L. Morlet in the MNHN collections with an original label stating "Type". In order to stabilize the name, a shell that matched well with the illustration and measurements given in the original description is designated here as lectotype MNHN-IM 200030873 (Fig. 3.3G).

Remarks

Haploptychius fischeri is currently known only from the north of Vietnam (Schileyko 2011, Do and Do 2015). The type specimen was examined. Shell thickened, oblique-heliciform with depressed spire. Shell surface with strong radial ridges; penultimate whorl rounded; last whorl axially deflected. Aperture subquadrangular, parietal lamella strong and parietal callus thickened. Peristome wide; lip thickened and reflected. Umbilicus narrowly open.

Compared with *H. pellucens* and *H. porrectus*, this species differs in its larger and thicker shell, depressed spire, prominent transverse ridges, subquadrangular aperture, thicker parietal lamella, and narrower umbilicus.

***Haploptychius blaisei* (Dautzenberg & Fischer, 1905)**

Figs 3.1, 3.4D–F; Table 3.1

Streptaxis blaisei Dautzenberg and Fischer 1905: 86, 87, pl. 3 figs 1–4. Type locality: Ile Krieu, Tonkin [Krieu Island, Ha Long, Quang Ninh Province, Vietnam].

Haploptychius blaisei—Kobelt 1906: 173, pl. 66, figs 4–7. Richardson 1988: 212.

Material examined

The original description was based on single specimen since stated "un seul examplaire" (a single example). The specimen of M. Blaise in the MNHN collections is considered as holotype MNHN-IM 200030866 (Fig. 3.4D).

Phu Ly, Dongson, Ha Nam, Vietnam: NHMUK Vermeulen coll. (4 shells). Tam Phatok, Ngoi, Luang Phrabang, Laos: CUMZ 6276 (1 shell; Fig. 3.4E), 6257 (15 shells; Fig. 3.4F).

Remarks

Shell oblique-heliciform, white and translucent. Whorls 6½; spire depressed to slightly convex, with distinct suture. Shell surface glossy, with thin transverse ridges that diminish below periphery and around umbilicus. Embryonic shell large, about 2½ whorls, with a smooth surface; following whorls regularly expanded. Penultimate whorl rounded; last whorl axially deflected. Aperture semi-ovate; peristome discontinuous, parietal callus thin; lip thickened and slightly expanded. Apertural dentition with one strong parietal lamella. Umbilicus widely open and shallow.

Haploptychius blaisei is superficially similar to *H. diespiter* (Mabille, 1887), and *H. dorri* from North Vietnam, but it has a larger shell, more depressed spire, rounded penultimate whorl, a wide and deep umbilicus, and thin transverse ridges on the upper periphery. For comparison, *H. diespiter* has the last whorl less deviated from the vertical axis, and *H. dorri* has a more depressed suture.

Genus *Perrottetia* Kobelt, 1905

Odontartemon (*Perrottetia*) Kobelt 1905: 91. Kobelt 1906: 108. Thiele 1931: 730. Forcart 1946: 215.

Oophana (*Perrottetia*)—Benthem Jutting 1954: 95.

Perrottetia—Zilch 1960: 562, 563, Richardson 1988: 237. Schileyko 2000: 777, 778. Siriboon et al., 2013: 44, 45.

Type species. *Helix peroteti* Petit, 1841: 100, by subsequent designation of Forcart (1946: 215).

Remarks

The genus *Perrottetia* differs from all other Southeast Asian streptaxid genera in having two longitudinal furrows outside the aperture. Apertural dentition usually comprises one or two parietal lamellae, plus, palatal, basal and columellar lamellae. Genitalia with long penis, penial hooks present, and vaginal hooks sometimes present (Zilch 1960; Schileyko 2000; Siriboon et al., 2013).

Currently, 29 *Perrottetia* species are recognized, from India and Sri Lanka to Indochina and southern China (Kobelt 1906, Richardson 1988, Schileyko 2011, Siriboon et al., 2013). Two species have been reported from Laos, *P. dugasti* (Morlet, 1892) and *P. daedaleus* (Bavay and Dautzenberg, 1908) (see Schileyko 2011).

***Perrottetia dugasti* (Morlet, 1892)**

Fig. 3.5A

Streptaxis dugasti Morlet 1892: 82. Morlet 1893[1892]: 315, 316, pl. 7, fig. 5, 5a, 5b. Type locality: Laï-Chau, sur les bords de la Riviére Noire, Tonkin [on the banks of the Black River, Lai Chau Province, Vietnam]. Gude 1903: 255.

Perrottetia dugasti—Kobelt 1906: 123, 124, pl. 61, fig. 13. Richardson 1988: 239. Schileyko 2011: 23.

Material examined

The species was described based on material from L. Dugast collection but no illustration was given. Morlet (1893: 315, 316, pl. 7, fig. 5, 5a, 5b) subsequently published the description and illustrated a single specimen. There is a specimen of L. Morlet in the MNHN collections with an original label stating "Type". In order to stabilise the name, the shell that closely matched with the measurements given in the original description and illustration in Morlet (1893: pl. 7, fig. 5, 5a, 5b) is here designated as lectotype MNHN-IM 200030867 (Fig. 3.5A).

Remarks

Shell sub-oblique heliciform with depressed spire and 6 whorls. Shell surface smooth, glossy and with a distinct suture. Embryonic shell smooth, following whorl regularly expanded. Last whorl rounded, axially deflected, with longitudinal furrows present. Aperture narrow; peristome discontinuous, thick and expanded, and short sinulus present. Aperture dentition consisting of two parietal lamellae (lower one large; upper one small and close to sinulus), one palatal lamella, one basal lamella and one bifid columellar lamella.

Compared with *P. messageri* (Bavay and Dautzenberg, 1908), this species differs in having a strong lower parietal lamella, a bifid columellar lamella, and the left periphery of penultimate whorl not extended beyond the diameter of the last whorl. In contrast, *P. messageri* has a strong columellar lamella, a supracolumellar lamella is present, and the left periphery of the penultimate whorl extended beyond the diameter of the last whorl (Fig. 3.5D).

***Perrottetia daedaleus* (Bavay & Dautzenberg, 1908)**

Fig. 3.5C

Streptaxis daedaleus Bavay and Dautzenberg 1908: 230. Type locality: Pac-Kha [Pa Kha, Son La Province, Vietnam]. Bavay and Dautzenberg 1909: 164, 165, pl. 4, figs 1–4.

Streptaxis daedaleus var. *major* Bavay and Dautzenberg 1908: 231. Type locality: Pac-Kha [Pa Kha, Son La, Vietnam]. Bavay and Dautzenberg 1909: 165.

Oophana daedaleus—Richardson 1988: 234. Schileyko 2011: 23.

Oophana daedaleus major—Richardson 1988: 234.

Material examined

Syntype of *Streptaxis daedaleus* var. *major* MNHN-IM 200030871 (Fig. 3. 5B). Tonkin: NHMUK 1909.6.9.118-9 (2 shells). Pac-Kha, Tonkin: NHMUK 1909.7.9.15-6 (2 shells), NHMUK Preston coll. date 7.4.09 (2 shells), Rolle coll. date 27.11.09 (3 shells). Long Ping, Tonkin: NHMUK Rolle coll. date 27.1.09 (2 shells).

Remarks

Shell suboblique-heliciform with a convex spire and 6 whorls. Shell surface with strong transverse ridges running continuously to umbilicus. Embryonic shell with thin transverse ridges and following whorl regularly expanded. Last whorl rounded, axially deflected, longitudinal furrows present. Aperture triangular; peristome discontinuous, thickened, broadly expanded and sinulus absent. Apertural dentition with two parietal lamellae (lower one small; upper one large and close to sinulus), one angular lamella, one palatal lamella (located far inside aperture) and one columellar lamella.

This species is superficially similar to *P. mabillei* (Bavay and Dautzenberg, 1903) in having strong transverse ridge over the entire shell, but *P. daedaleus* has a large upper parietal lamella, a palatal lamella located inside the aperture, and strong columellar lamellae, while *P. mabillei* has a large lower parietal lamella and bifid columellar lamellae (Fig. 3.5B).

***Perrottetia aquilonaria* Siriboon & Panha, 2013**

Figs 3.1, 3.5E

Perrottetia aquilonaria Siriboon et al., 2013: 50–52, figs 3D–H, 4D–F: Type locality: Wat Tam Pha Plong, Chiangdao, Chiangmai, Thailand.

Material examined

Holotype CUMZ 5003, paratypes CUMZ 5004 (4 shells). Ban Namone, Xayabouly, Laos: CUMZ 6278 (2 shells; Fig. 5E), CUMZ 6279 (1 specimen in ethanol). Ban Bo Khoun, Boun Neua, Phongsaly, Laos: CUMZ 6280 (1 shell).

Remarks

Perrottetia aquilonaria was described from several localities in the northern part of Thailand with a complete information on shell, radula and genitalia. The specimens collected from limestone outcrops in Borkeo and Phongsaly of Laos have both shells and genitalia that match very well with this species. Laos specimens seem to differ only in the slightly smaller shell, therefore we treated them as the same species.

Perrottetia aquilonaria can be distinguished from *P. dugasti* and *P. messageri* from Vietnam by having a depressed spire, shouldered last whorl, thin parietal callus and upper-parietal lamella separated at a right angle. In contrast, *P. dugasti* has a rounded last whorl and a small upper-parietal lamella located deeper inside the aperture, and *P. messageri* has paralleled parietal lamellae, a small supercolumellar lamella is present, and the left side of the penultimate whorl extended beyond the diameter of the last whorl (Fig. 3.5A, D).

Perrottetia unidentata **Inkhavilay & Panha sp. n.**

Figs 3.1, 3.5F–I, 3.7E, F, 3.10A–F, I; Table 3.1

Type material

Holotype CUMZ 6281 (Fig. 3.5F). Measurement: shell height 5.3 mm, shell width 9.7 mm and 6½ whorls. Paratypes CUMZ 6282 (4 shells; Fig. 3.5G), CUMZ 6283 (1 specimen in ethanol; Figs 3.7E, F, 3.9A–F, I), NHMUK 20160250 (2 shells).

Other material examined

Tam Than Kaisone, Viengxay, Houaphanh, Laos: CUMZ 6284 (5 shell; Fig. 3.5I), CUMZ 6285 (2 shells; Fig. 3.5H).

Type locality

The limestone outcrop at Ban Nawit, Viengxay, Houaphanh, Laos (20°22'37.3"N, 104°16'43.2"E) about 700 meters above mean sea level.

Diagnosis

This new species differs from *P. daedaleus*, *P. aquilonaria*, *P. dugasti* and *P. messageri* from Vietnam in having an oblique shell, a single parietal lamella, widely expanded lip, the last whorl strongly axially deflected, the left side of penultimate whorl well extended beyond the diameter of last whorl, and the distal end of penis with a wing-like structure. The other four species have two parietal lamellae, the last whorl little axially deflected and the left side of penultimate whorl not extended beyond the diameter of the last whorl. For further comparison, *P. daedaleus* has an elevated spire, transverse ridges over the entire shell and a basal lamella located deep inside aperture (Fig. 3.5C); *P. aquilonaria* has a smaller shell, elevated spire, bifid columellar lamella, and genitalia with atrial pores and vaginal hooks absent (Fig. 3.5E);

P. dugasti and *P. messageri* have a smooth shell surface, a bifid collumella lamella and a supracolumellar lamella (Fig. 3.5A, D). *Perrottetia gudei* from north Vietnam differs from the new species in having an elevated spire, in being less deviated from the vertical axis, and in having thin transverse ridges (see Siriboon et al., 2013).

Description

Shell oblique-heliciform, semi-transparent; whorls 6½, spire weakly convex with distinct suture. Shell surface glossy with strong transverse ridges on upper shell surface. Embryonic shell large, about 2½ whorls, with a smooth surface; following whorls regularly coiled. Shell periphery shouldered; last whorl axially deflected; two deep longitudinal furrows present. Aperture semi-ovate; peristome discontinuous; parietal callus thin; lip thickened, broadly expanded and slightly reflected. Apertural dentition with one large, strong and sinuous parietal lamella, one small upper palatal lamella, one palatal lamella, one large basal lamella, one strong columellar lamella, and one small supracolumellar lamella. Umbilicus widely open and shallow (Fig. 3.5F–I).

Radula

Each row consists of 26-38 teeth with formula (13-19)-1-(13-19). Central tooth small and triangular, with pointed cusp. Lateral and marginal teeth undifferentiated, lanceolate, unicuspid. Latero-marginal teeth gradually reduce in size, with outermost teeth much smaller and shorter than inner teeth (Fig. 3.10I).

Genital organs

Atrium (at) short. Proximal penis (p) long and slender; distal part near retractor muscle with an expanded wing-like structure (a flat blade on either side of the penis, each about one-tenth of penis length). Penial sheath (ps) thin and extending about one-third of penis length; penial sheath retractor muscle (psr) very thin, originating at

atrium and inserting distally on penial sheath (Fig. 3.7E). Vas deferens (vd) passes through about one-third of penial sheath length before entering into penis apically (Fig. 3.7F). Penial retractor muscle (pr) thin and long, inserted at penis and vas deferens junction.

Internal wall of atrium generally smooth (Fig. 3.10A). Penial wall densely covered with light brown penial hooks, about 20 hooks/200 μm^2; hooks located on low elliptical penial papillae. Penial hooks small (< 0.1 mm in length), slender, expanded at base, tips pointed and curved towards genital orifice (Fig. 3.10B–D).

Vagina (v) short, about one-tenth of penis length. Gametolytic duct (gd) a long tube extending as far as albumin gland; gametolytic sac (gs) ovate. Free oviduct (fo) long and cylindrical with equivalent diameter to vagina, tapering distally. Oviduct (ov) enlarged and folded; prostate gland inconspicuous and bound to oviduct. Talon (ta) very small, short and club shape. Hermaphroditic duct (hd) bearing very short and thin seminal vesicle (sv) about one and half times longer than the length from talon to branching point of seminal vesicle (Fig. 3.7E).

Vaginal wall with transparent vaginal hooks (about 10 hooks/200 μm^2). Hooks located on low conical vaginal papillae. Vaginal hooks small (< 0.1 mm in length), short and expanded at base; tips pointed and straight to slightly curving away from genital orifice (Fig. 3.10E, F).

Etymology

The specific epithet "*unidentata*" derived from the Latin words "*unus*" meaning "one" and "*dens*" meaning "tooth". It referred to a single parietal lamella (or teeth) of the new species.

Distribution

This species is known only from the type locality, Houaphanh, a limestone karst area.

Remarks

Shell variation is evident from specimens from Tam Than Kaisone, about 20 km west of the type locality (Fig. 3.5H, I; CUMZ 6284, 6285). They are smaller, with a sinuous parietal lamella, and sometimes lack the upper palatal lamella (Table 3.1). However, only five shells and no living specimens were collected, so we provisionally identifying them as the same species.

***Perrottetia megadentata* Inkhavilay & Panha sp. n.**

Figs 3.1, 3.6A, B; Table 3.1

Type material

Holotype CUMZ 6286 (Fig. 3.6A). Measurement: shell height 7.1 mm, shell width 8.2 mm, and with 6 whorls. Paratypes: CUMZ 6287 (31 shells; Fig. 3.6B), CUMZ 6288 (2 shells), NHMUK 20160251 (2 shells), NUOL (2 shells), SMF (2 shells).

Type locality

The limestone outcrop at Ban Phone Can, Yommalat, Khammouan, Laos (17°31'35.6"N, 105°9'40.7"E)

Diagnosis

The characters distinguishing *Perrottetia megadentata* sp. n. from *P. daedaleus*, *P. aquilonaria*, *P. dugasti* and *P. mabillei* are a single large parietal lamella, the absence of a palatal lamella absent and the presence of an infra-columellar lamella. The other four species have two parietal lamellae and a palatal lamella. Furthermore, *P. dugasti*

and *P. aquilonaria* have a smooth shell, slightly depressed spire, and a bifid columellar lamella (Fig. 3.5A, E). *Perrottetia daedaleus* and *P. mabillei* have strong transverse ridges over the entire shell, a palatal lamella, and a bifid basal lamella, a columellar lamella is absent in *P. mabillei* (Fig. 3.5B), while one basal and one columellar lamella are present in *P. daedaleus* (Fig. 3.5C). The new species differs from *P. unidentata* sp. n. in its ovate shape, smooth shell surface, thicker shell, in the absence of a palatal lamella, and in having infra- and supra-columellar lamellae. The new species is superficially similar to *P. dermapyrrhosa* Siriboon and Panha, 2013, but is distinguished by having a single and large parietal lamella, and in the absence of a palatal lamella.

Description

Shell oblique-ovate, white and translucent; whorls 6, spire conical, with distinct suture. Shell surface glossy with transverse ridges near suture. Embryonic shell large, about 2½ whorls, with a smooth surface; following whorls regularly coiled. Shell periphery rounded; last whorl axially deflected; two shallow and short longitudinal furrows present. Aperture subcircular, peristome continuous; parietal callus thickened; lip thickened, expanded and reflected; short sinulus present. Apertural dentition with very large and strong sinuous parietal, one large basal lamella located deep inside aperture, one small infracolumellar lamella, one large columellar lamella, and one small supracolumellar lamella. Umbilicus widely open and deep
(Fig. 3.6A, B)

Etymology

The specific epithet "*megadentata*" is derived from the Greek word "*mega*" meaning "large" and the Latin word "*dens*" meaning "tooth". It referred to the single large parietal lamella of the new species.

Distribution

This species is known only from the type locality in central Laos.

Remarks. To date no living specimens have been collected.

Genus *Indoartemon* Forcart, 1946

Oophana (Indoartemon) Forcart 1946: 215. Benthem Jutting 1954: 95.

Indoartemon—Zilch 1960: 562. Richardson 1988: 223. Schileyko 2000: 776, 777. Siriboon et al., 2014b: 162.

Type species. *Streptaxis eburnea* Pfeiffer, 1861 by original designation.

Remarks

The genus *Indoartemon* can be recognized by the dentition, which consists of one parietal and one palatal lamella (a basal lamella is also present in some species). The penis is long, with a thin penial sheath extending about half of the penis length, through which the vas deferens does not pass. Penial hooks are present (Siriboon et al., 2014b).

Currently, ten species are recognized, of which seven were reported from Indochina south of China and Hainan. Only one species, *I. tridens* (Möllendorff, 1898) has previously been recorded from Laos (Richardson 1988, Schileyko 2000, Siriboon et al., 2014b); here we describe another.

Indoartemon tridens (Möllendorff, 1898)

Figs 3.1, 3.6C

Streptaxis tridens Möllendorff 1898: 67. Type locality: Boloven, Laos [=Boloven Plateau, Paksong, Champasak, Laos]. Gude 1903: 220.

Odontartemon tridens—Kobelt 1905: 94, 95, pl. 58, figs 19, 20.

Indoartemon tridens—Zilch 1961: 85, pl. 5, fig. 15. Richardson 1988: 225. Schileyko 2011: 23.

Material examined. Holotype SMF 108507 (Fig. 3.6C).

Remarks

Shell oblique-ovate with 5½ whorls, semi-transparent, spire slightly convex, with distinct sutures. Shell surface glossy white with thin growth lines; following whorls regularly coiled. Last whorl axially deflected. Aperture triangular; peristome continuous; lip thickened, little expanded and slightly reflected. Apertural dentition with one large parietal lamella, one palatal lamella, and one small bifid columellar lamella.

Only the type specimen was examined. *Indoartemon tridens* differs from *I. eburneus*, *I. prestoni* (Gude, 1903) and *I. medius* Siriboon and Panha, 2014 from Thailand by having a bifid columellar lamella, an ovate-heliciform shape, its smooth shell surface, narrow umbilicus, and having the left side of penultimate whorl extended beyond the diameter of last whorl. For comparison, *I. eburneus* and *I. prestoni* have a less deviated last whorl, transverse ridges on the shell, and a widely open umbilicus; *I. medius* has an angular penultimate whorl and strong transverse ridges.

***Indoartemon diodonta* Inkhavilay & Panha, sp. n.**

Figs 3.1, 3.6D–F; Table 3.1

Type material

Holotype CUMZ 6289 (Fig. 3.6D). Measurement: shell height 7.5 mm, shell width 8.3 mm, and with 7 whorls. Paratypes: CUMZ 6290 (44 shells; Fig. 3.6E, F), NHMUK 20160252 (2 shells), NUOL (2 shells), SMF (2 shells).

Other material examined

Tam Nang Ann, Tha Khek, Khammouan, Laos: CUMZ 6291 (7 shells). Tam Xieng Lieb, Tha Khek, Khammouan, Laos: CUMZ 6292 (15 shells).

Type locality

Tam Xang, Tha Khek, Khammouan, Laos, 17°25'44.0"N, 104°51'49.1"E.

Diagnosis

This new species superficially resembles *I. eburneus* and *I. prestoni* from Thailand, but it differs in having a much smaller shell, an oblique-heliciform shape, open umbilicus, and the last whorl is strongly deviated from the vertical axis. This species differs from *I. medius* from Thailand in its smaller shells, angular penultimate whorl and thin transverse ridges. *Indoartemon diodonta* sp. n. differs from *I. bidens* (Möllendorff, 1883) from Hainan and *I. tridens* by having fine transverse ridges on the upper periphery, and the last whorl is less deviated from the vertical axis. These two species also have a smooth shell surface and a more strongly deviated last whorl, and a bifid columellar lamella is present in *I. tridens*.

Description

Shell oblique-heliciform, white and translucent; whorls 6½–7, spire conical, with distinct suture. Shell surface dull, with fine transverse ridges that diminish below the periphery. Embryonic shell large, about 2½ whorls, with smooth surface; following

whorls regularly coiled. Last whorl shouldered, axially deflected, and not expanded. Aperture subcircular; peristome continuous, parietal callus thickened; lip thickened, expanded and little reflected. Apertural dentition with one large and strong parietal and one small palatal lamellae. Umbilicus narrow and deep
(Fig. 3.6D–F).

Etymology

The specific epithet "*diodonta*" is derived from the Greek word "*di*" meaning "two" and the Latin word "*odontos*" meaning "tooth", referring to the dentition of the new species.

Distribution

This species is known from limestone karst in Khammouan Province, central Laos. The animals can be found at altitudes up to 140 meters above mean sea level.

Remarks. To date no living specimens have been collected.

Discussion

This study increases the number of streptaxid species recorded from Laos to twelve, three of which are new. Streptaxids occur in both limestone and non-limestone areas in the central and northern parts of Laos. The fauna apparently remains less diverse than that of Thailand and Vietnam (Panha 1996, Hemmen and Hemmen 2001, Siriboon et al., 2013, 2014a, b; Schileyko 2011). The highly modified habitats of southern and some central areas of Laos may harbour a lower species diversity. For example, *Indoartemon tridens* was recorded in 1898 by Möllendorff from its type locality at Boloven plateau, Paksong, Champasak, Laos, but our surveys yielded no specimens collected from this locality.

The species can be separated by geography, shell morphology, and (where available) genital anatomy. Two species from the genus *Haploptychius*; *H. pellucens* and *H. porrectus* were described from Laos by Pfeiffer (1863). From our results living and shells specimens of *H. pellucens* and *H. porrectus* were collected from nine sampling sites in six provinces such as Louang Namtha, Oudomxay, Louang Phrabang, Xayabouly, Bolikhmaxay and Xieng Khaung. Shell morphology and genitalia anatomy were compared between the two species. The two can be separated by having different shell size and shape, as well as differences in the penial sheath, penial hooks, and vaginal wall. The southernmost population of *H. pellucens* is particularly small. Most records of *Haploptychius* species are from northern Laos, latitude 18°-21°.

Perrottetia unidentata sp. n. and *P. megadentata* sp. n. are the first two species of the genus recorded in Laos, and are geographically and altitudinally separated. *Perrottetia unidentata* sp. n. occurs in northern Laos close to the Lao-Vietnam border at over 700 m above sea level, while *P. megadentata* sp. n. occurs far to the south and lower than 200 m above sea level (Fig. 3.1). The two species can be separated by shell morphology. *Perrotettia* has been collected from central to northern Laos, latitude 18°-22°.

Indoartemon diodonta sp. n. is the second species of this genus recorded from Laos after *I. tridens* (Möllendorff 1898). The new species was found in central Laos, while the first was found in southern Laos, at over 1000 m above sea level. In Laos, *Indoartemon* has now been recorded between latitude 14°-18°.

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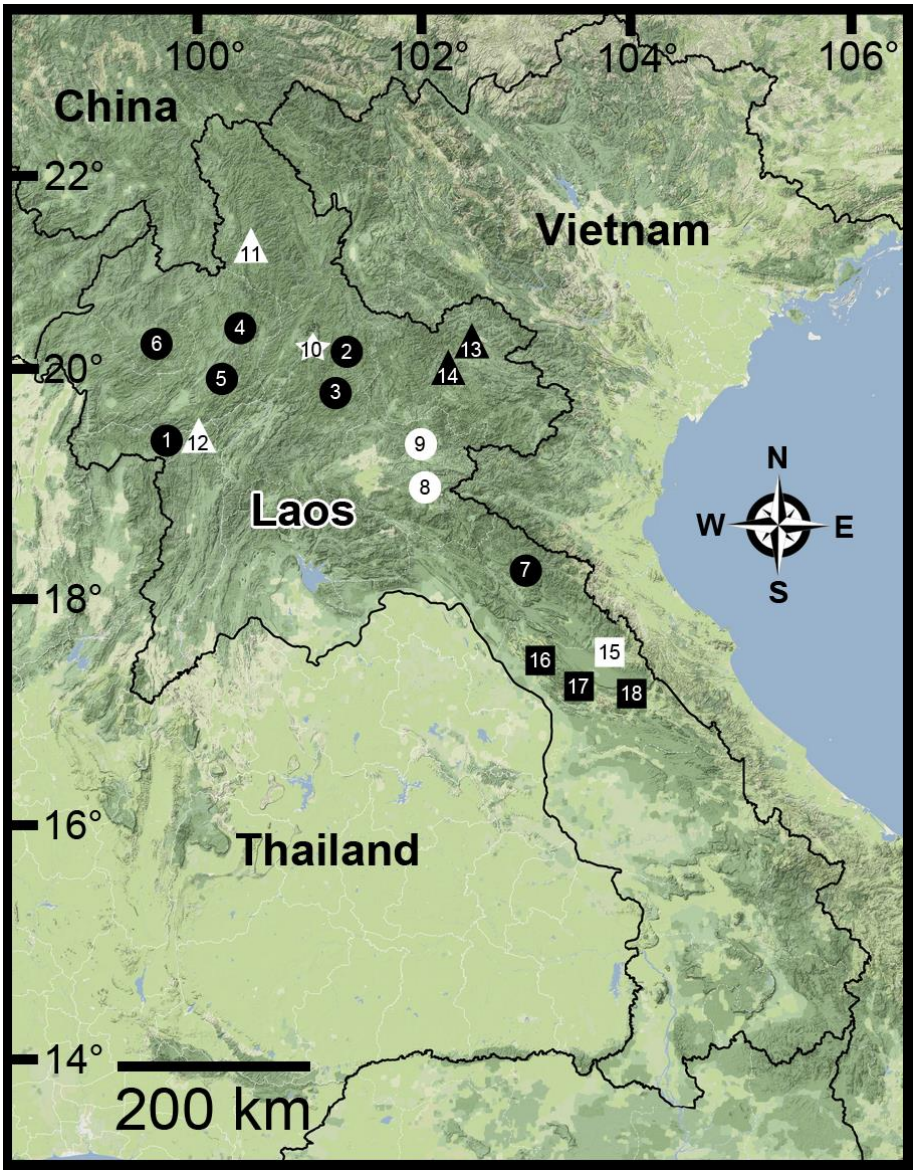

Figure 3.1 Approximate locations of the type locality of *Haploptychius* spp., *Perrottetia* spp., and *Indoartemon* spp. in Laos. Described species (**black circle**) *Haploptychius pellucens*, (**white circle**) *Haploptychius porrectus*, (**star**) *Haploptychius blaisei*, (**white triangular**) *Perrotettia aquilonaris*, (**black triangular**) *P. unidenta* sp. n., (**white rectangular**) *P. megadenta* sp. n. and (**black rectangular**) *Indoartemon diodonta* sp. n. The numbered localities are detailed in Table 1, except locality no. 6 is from Tam Kao Rao, Vieng Phoukha, Luang Namtha, Laos, and no. 11 from Ban Bo Khoun, Boun Neua, Phongsaly, Laos.

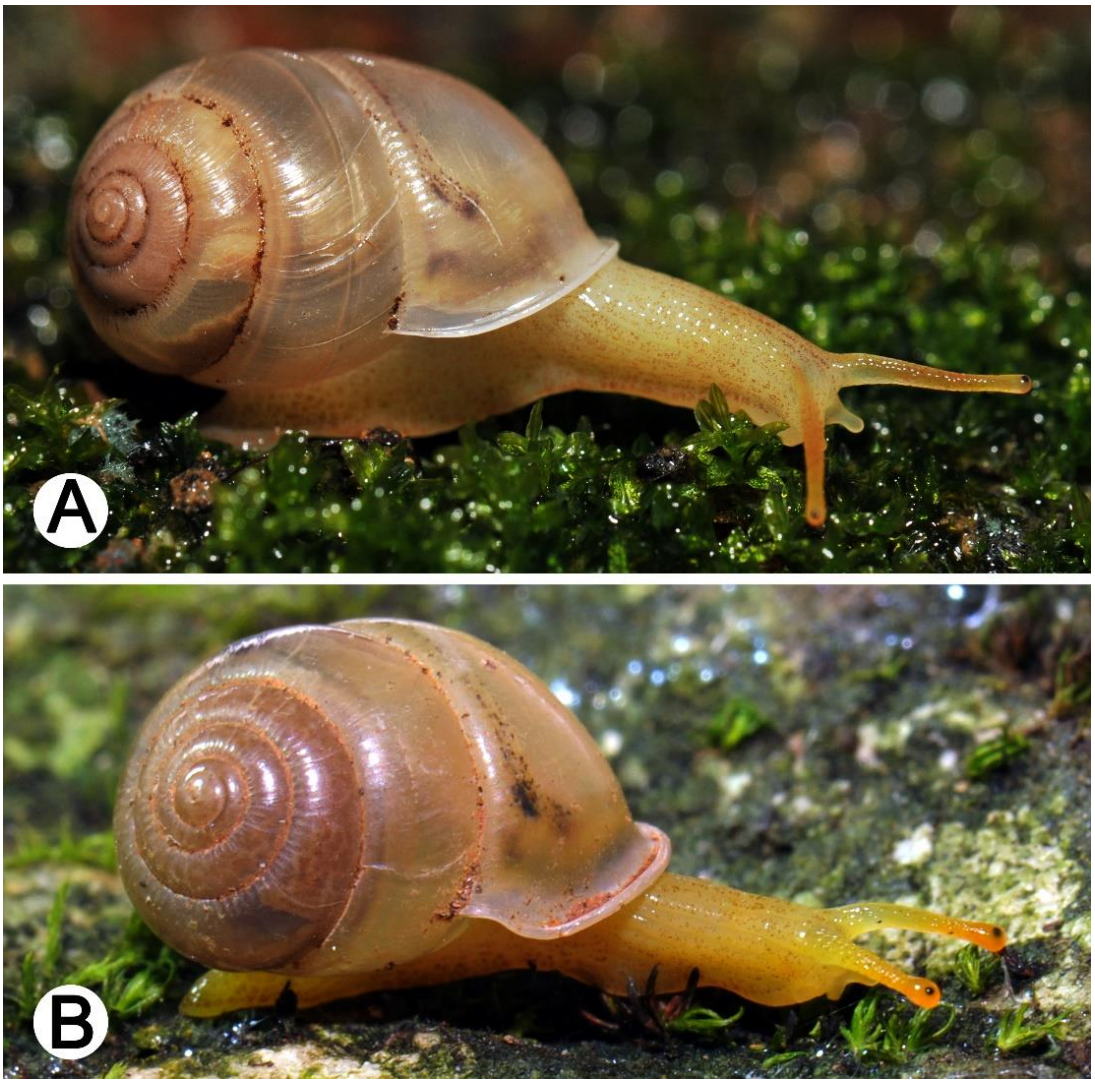

Figure 3.2 Living snails of **A** *Haploptychius pellucens* CUMZ 6265, from Xayabouly (shell width about 11 mm) and **B** *Haploptychius porrectus* CUMZ 6273, from Xieng Khuang (shell width about 7 mm).

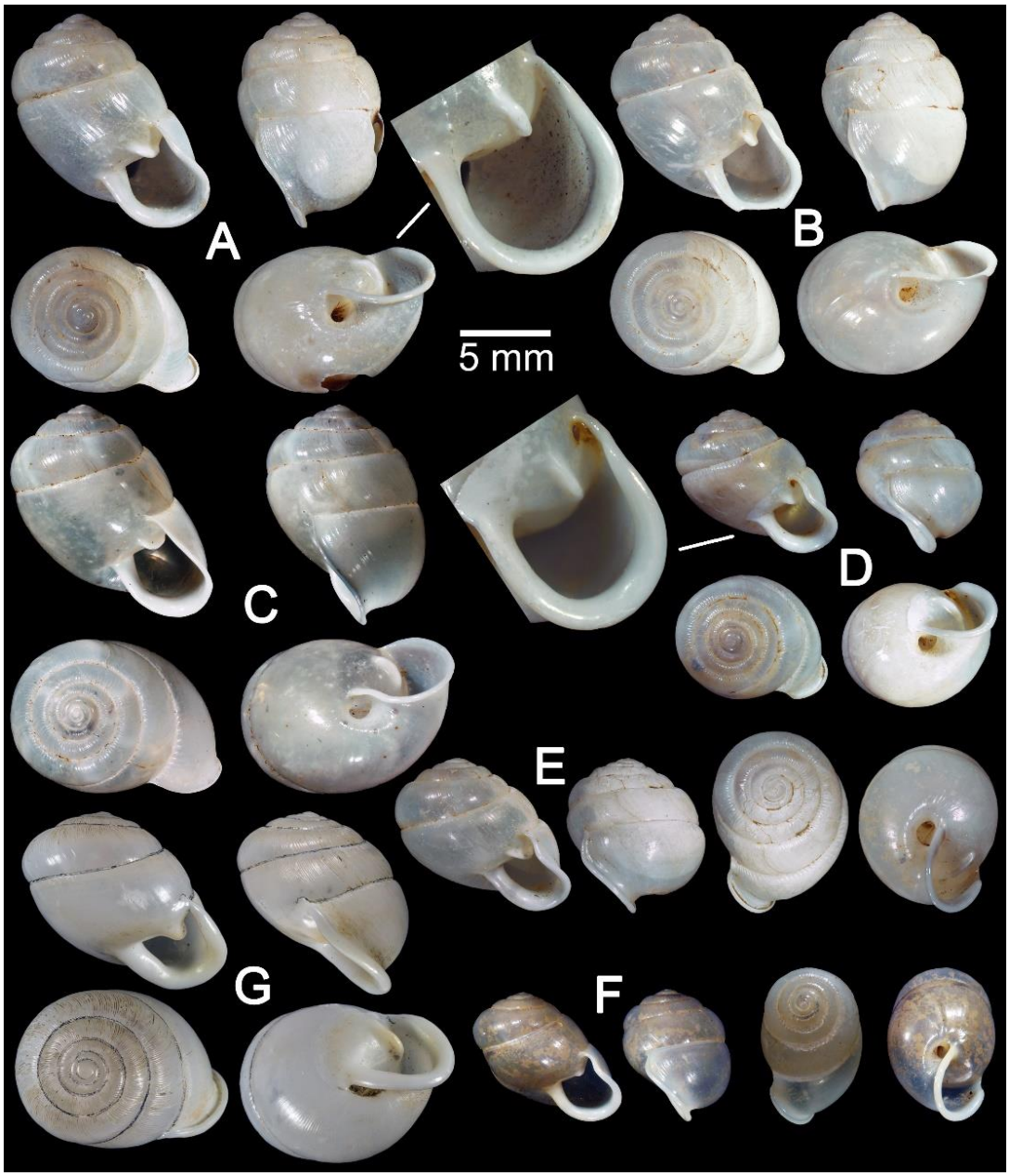

Figure 3.3 Shells of *Haploptychius* spp. **A–C** *Haploptychius pellucens* **A** lectotype NHMUK 20160249.1 with apertural dentition **B** paralectotype NHMUK 20160249.2, and **C** specimen CUMZ 6264, from Xayabuly. **D–F** *Haploptychius* porrectus **D** lectotype NHMUK 20140750.1 **E** paralectotype NHMUK 0140750.2 , and **F** specimen CUMZ 6273, from Xieng Khuang **G** *Haploptychius fischeri,* lectotype MNHN-IM-2000-30873.

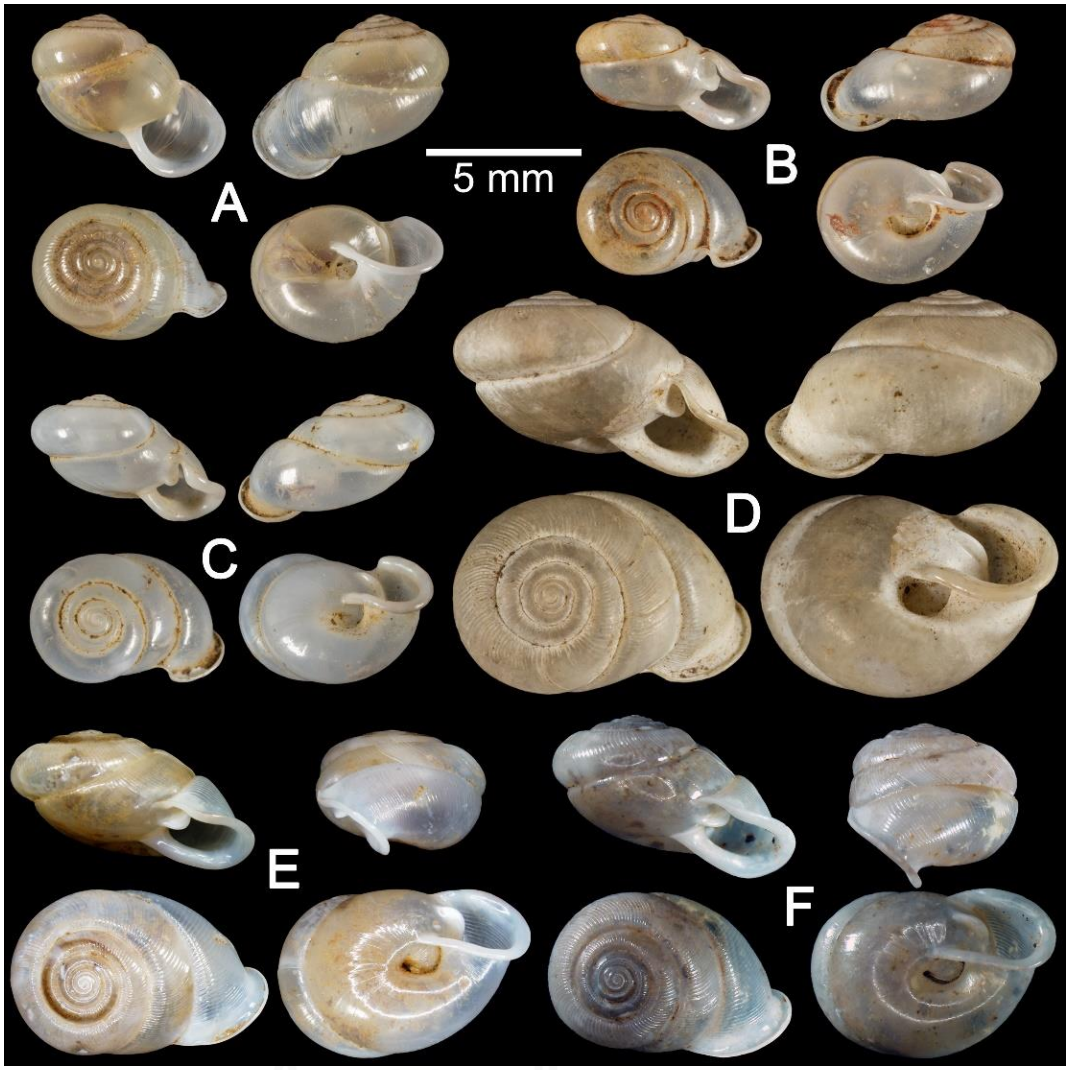

Figure 3.4 Shells of *Haploptychius* spp. **A** *Haploptychius anceyi* lectotype MNHN-IM-2000-30868. **B** *Haploptychius diespiter* lectotype MNHN-IM-2000-30870. **C** *Haploptychius dorri* lectotype MNHN-IM-2000-30869. **D-F** *Haploptychius blaisei* **D** holotype MNHN-IM-2000-30866 and **E-**F specimens from Luang Phrabang CUMZ 6257.

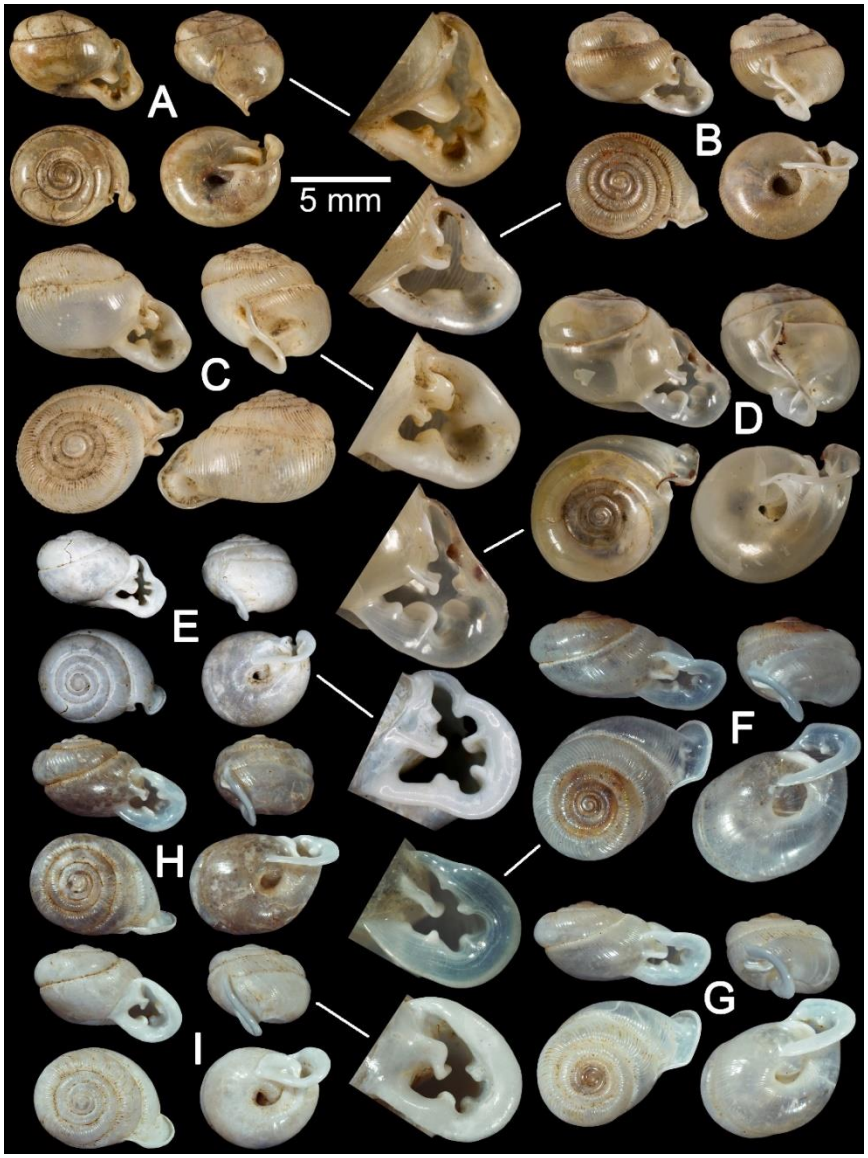

Figure 3.5 Shells of *Perrottetia* spp. **A** *Perrottetia dugasti* lectotype MNHN-IM-2000-30867. **B** *Perrottetia mabillei* syntype MNHN-IM-2000-30874. **C.** *Perrottetia daedaleus* var. *major* syntype MNHN-IM-2000-30871 **D** *Perrottetia messageri*, syntype MNHN-IM-2000-30875. **E** *Perrottetia aquilonaris* specimen CUMZ 6278 from Xayabouly with apertural dentition. **F, G** *Perrottetia unidenta* sp. n. **F** holotype CUMZ 6281 with apertural dentition and **G** paratype CUMZ 6282. **H, I** *Perrottetia unidenta* sp. n. specimens from Tam Than Kaisone **H** specimen with upper palatal CUMZ 6284 and **I** specimen without upper palatal CUMZ 6285.

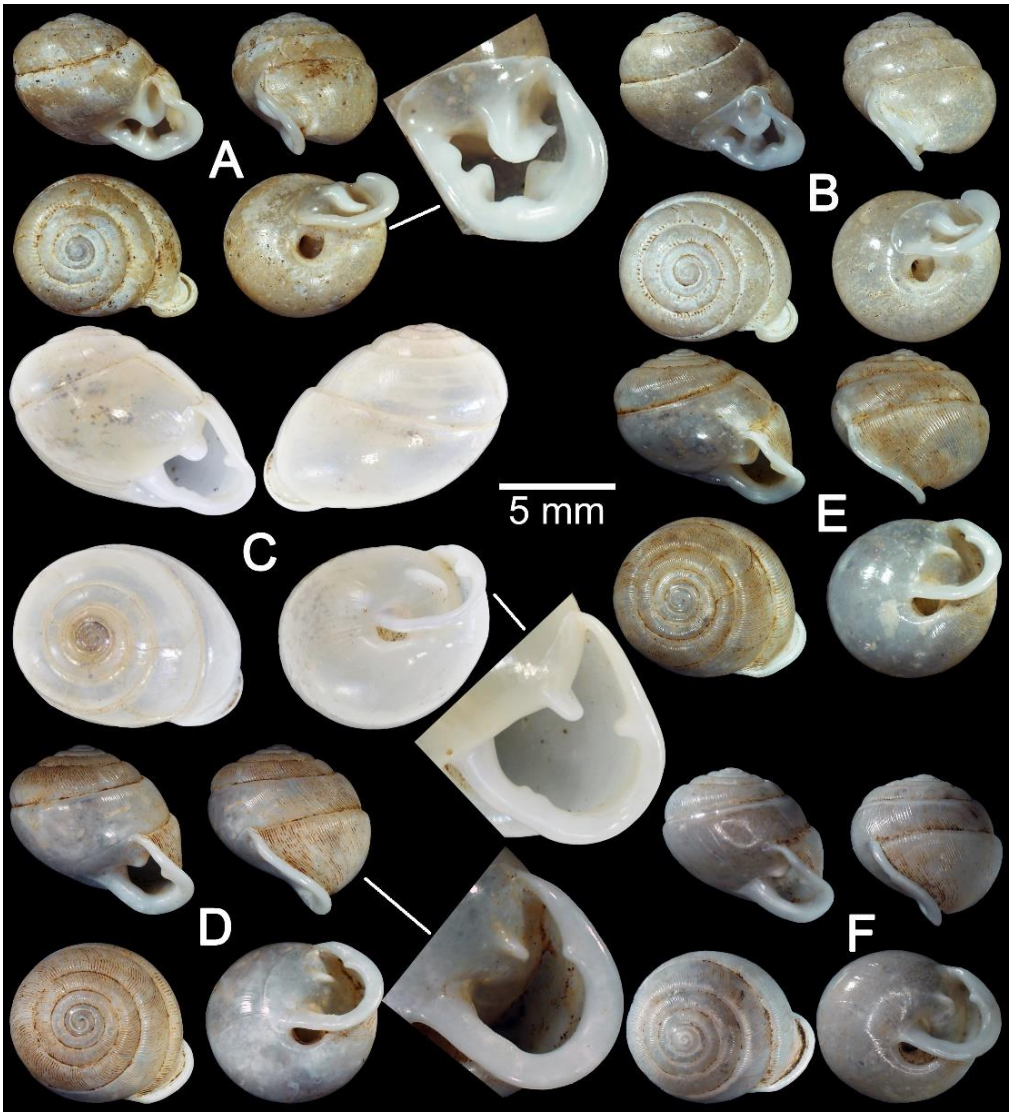

Figure 3.6 Shells of *Perrottetia* and *Indoartemon* spp. **A, B** *Perrottetia megadenta* sp. n. **A** holotype CUMZ 6286 with apertural dentition, and **B** paratype CUMZ 6287 **C** *Indoartemon tridens* holotype SMF 108507/1 with apertural dentition. **D–F** *Indoartemon diodonta* sp. n. **D** holotype CUMZ 6289 with apertural dentition, **E** paratypes CUMZ 6290, and **F** specimen from Tam Nang Ann, Tha Khek, Khammouan CUMZ 2691.

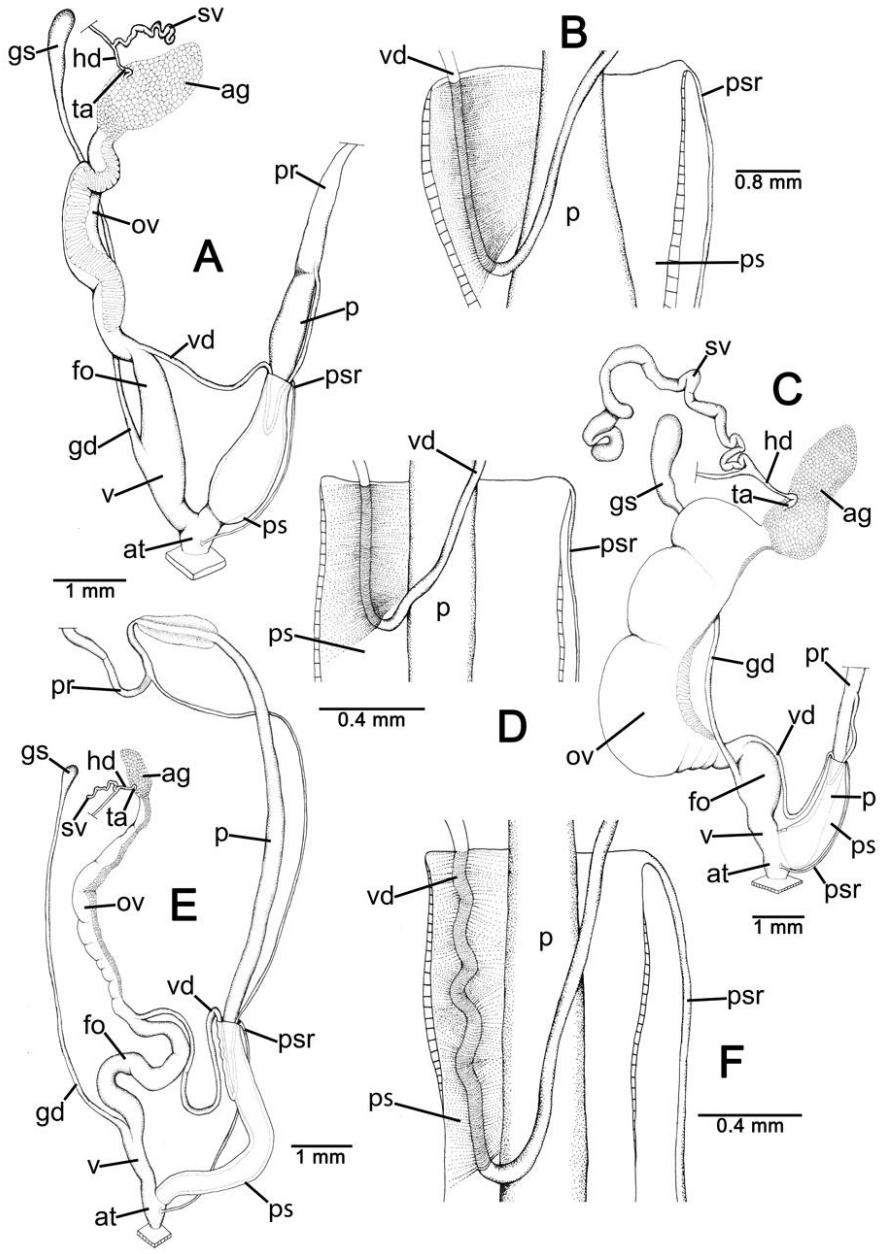

Figure 3.7 Genitalia of *Haploptychius* and *Perrottetia* species. **A, B** *Haploptychius pellucens* CUMZ 2670 **A** reproductive system, and **B** insertion of vas deferens into penial sheath **C, D** *Haploptychius porrectus* CUMZ 6274 **C** reproductive system, and **D** insertion of vas deferens into penial sheath **E, F** *Perrottetia unidenta* sp. n. CUMZ 6283 **E** reproductive system, and **F** insertion of vas deferens into penial sheath.

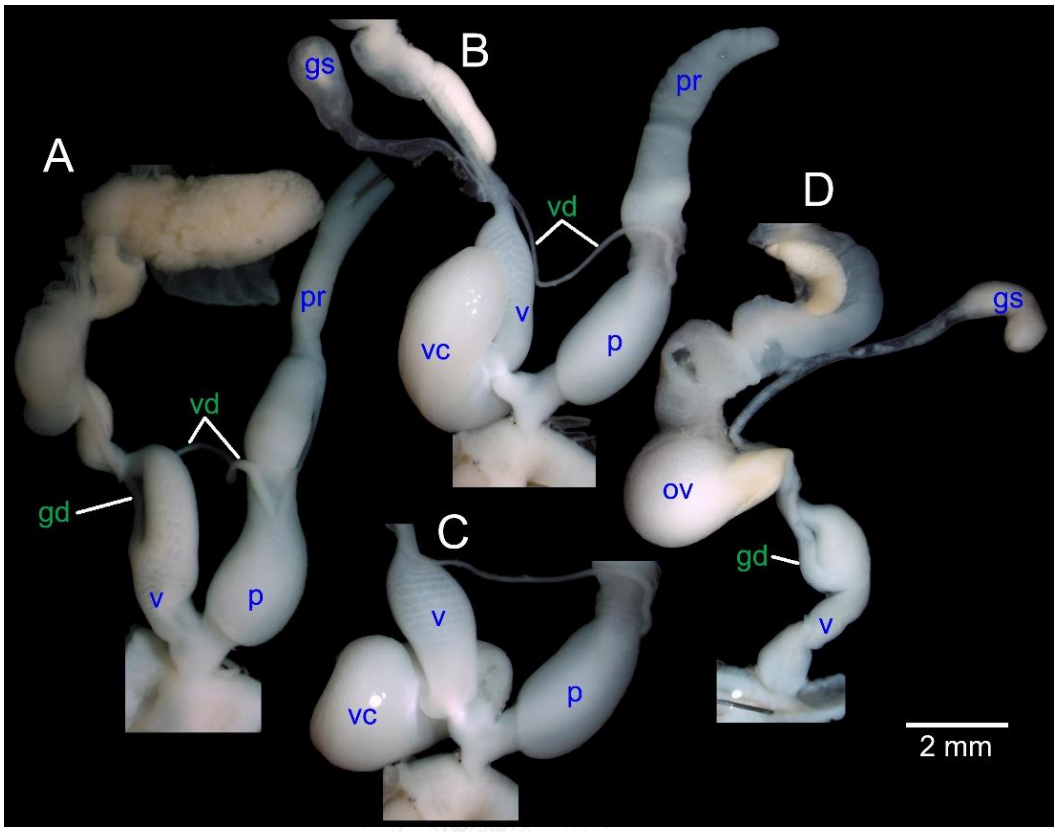

Figure 3.8 Genitalia of *Haploptychius pellucens* **A** completed reproductive system CUMZ 2670 **B, C** completed reproductive system with vaginal appendix CUMZ 6265, and **D** aphallus reproductive system CUMZ 6265.

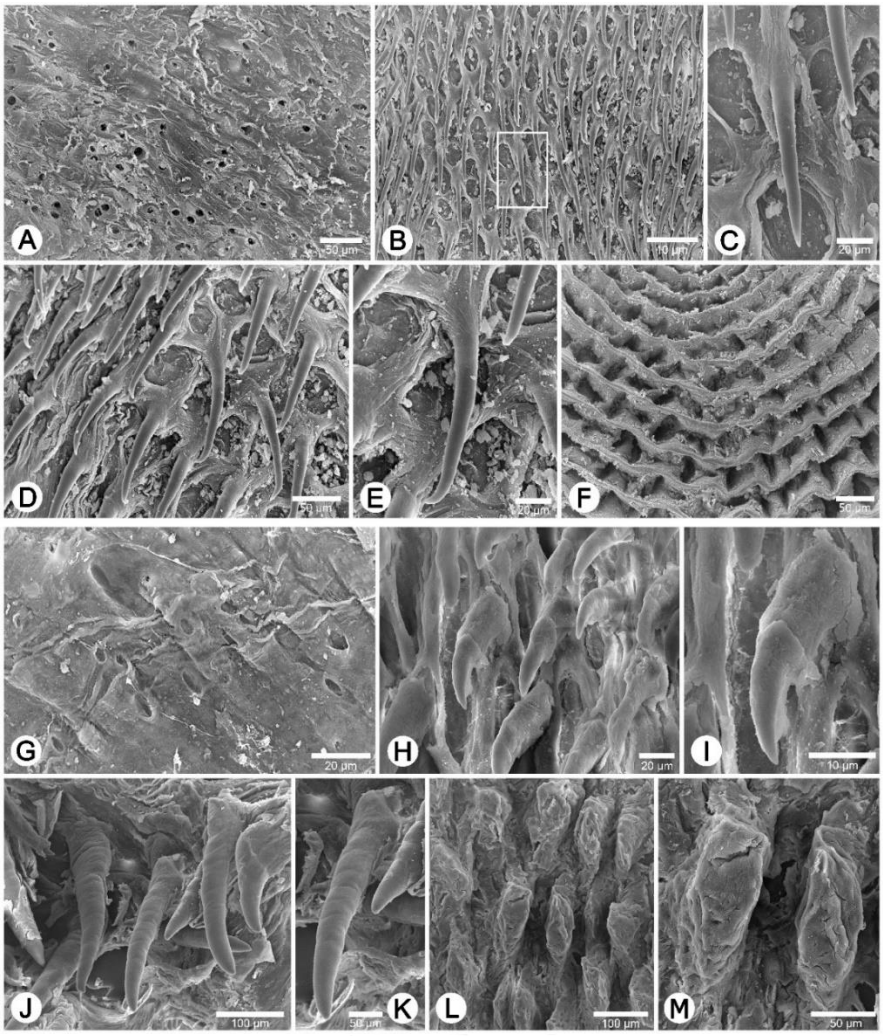

Figure 3.9 Internal sculpture of genitalia of *Haploptychius* spp. **A–F** *Haploptychius pellucens*, CUMZ 2670 **A** details of atrium surface **B** low magnification shows arrangement of penial hooks **C** top view of penial hook (from white square in **B**) **D** high magnification shows arrangement of penial hooks **E** lateral view of penial hook, and **F** arrangement of undulated parallel vaginal folds **G–M** *Haploptychius porrectus* specimen CUMZ 6275 **G** details of atrium surface **H** low magnification shows arrangement of penial hooks in distal area **I** lateral view of penial hook in distal area **J** high magnification shows arrangement of penial hooks in proximal area **K** lateral view of penial hook in proximal area **L** low magnification shows arrangement of papilla vaginal folds, and **M** high magnification shows arrangement of vaginal folds.

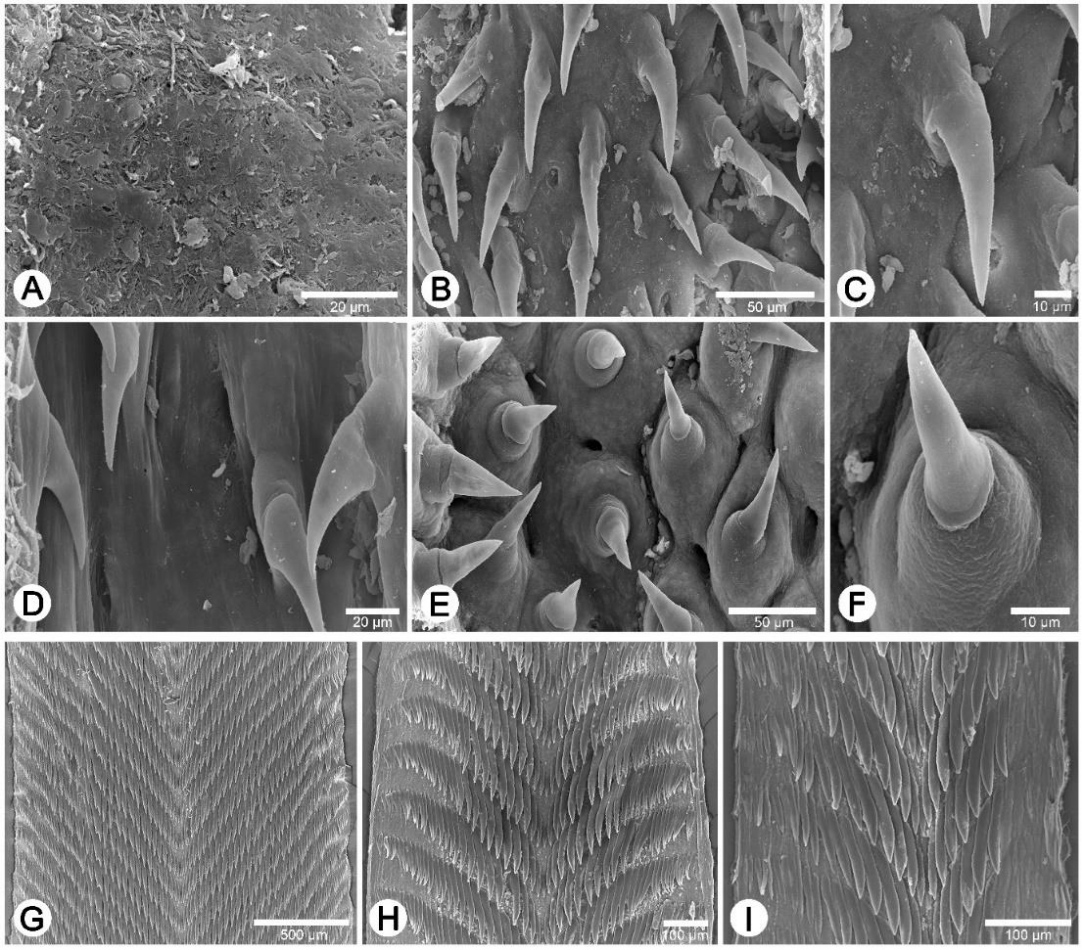

Figure 3.10 Internal sculpture of genitalia of **A–F** *Perrottetia unidenta* sp. n. paratype CUMZ 6283 **A** details of atrium surface **B** high magnification shows arrangement of penial hooks **C** top view of penial hook **D** lateral view of penial hooks **E** high magnification shows arrangement of vaginal hooks, and **F** top view of vaginal hook. Radula morphology of **G** *Haploptychius pellucens* specimen CUMZ 2670 **H** *Haploptychius porrectus* specimen CUMZ 6275, and **I** *Perrottetia unidenta* sp. n. paratype CUMZ 6283.

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Table 3.1 Shell measurements for populations of the three *Haploptychius*, four *Perrottetia*, and one *Indoartemon* species collected

Specie and locality and CUMZ nos	No. of specimens	Rangs, mean ± S.D. in mm of:				Number of whorls
		Shell height (H)	Shell width (W)	H/W ration	Shell angle	
Haploptychius pellucens (Pfeiffer, 1863)						
Lectotype and paralectotypes	3	11.1–13.0 11.9±1.02	10.6–13.3 11.7±1.45	0.9–1.0 1.0±0.01	31.7–37.1 34.9±2.77	6–6½
1. Ban Namone, Xayabouly District, Xayabouly, Laos (about 40 Km. from Ngeun District, Lao-Thai border to Xayabouly): (6264, 6265)	12	10.1–12.10 11.0±0.55	9.6–12.0 10.6±0.63	0.9–1.18 1.0±0.09	33.6–53.02 44.2±5.26	6–6½
2. Tam Phatok, Ngoi District, Luang Phrabang, Laos: (6267)	7	9.5–10.7 9.8±0.43	9.0–10.7 9.8±0.75	0.9–1.1 1.0±0.11	45.8–56.9 50.9±3.75	6–6½
3. Ngoi District, Luang Phrabang, Laos: (6268)	7	9.7–12.4 11.1±0.90	10.4–11.8 10.9±0.48	0.9–1.1 1.0±0.01	48.8–54.1 51.2±1.91	6½
4. Nam Ork Roo, Nathong, Namor District, Oudomxay, Laos: (6269, 6270)	35	9.5–11.5 10.2±0.53	9.3–12.0 10.8±0.61	0.8–1.1 0.9±0.08	42.5–54.1 48.9±3.19	6½
5. Ban Oudom, Pak Beng District, Oudomxay, Laos: (6271)	15	10.6–13.1 12.0±0.77	9.5–12.8 11.2±0.76	0.8–1.3 1.0±0.12	37.6–58.3 47.9±5.21	6½–7
7. Tam Mungkorn, Khamkeurt District, Bolikamxay, Laos: (6266)	4	8.8–9.6 9.3±0.30	8.0–9.1 8.7±0.50	1.0–1.1 1.0±0.03	46.7–50.3 48.2±1.56	6½–7
Haploptychius porectus (Pfeiffer, 1863)						
8. Ban Nong Tang, Phou kood District, Xieng Khuang, Laos: (6273, 6274)	19	6.2–8.1 7.4±0.50	6.3–8.4 7.4±0.52	0.8–1.2 0.9±0.11	41.1–59.6 49.6±4.58	6½
9. Tam Pew, Kham District, Xieng Khuang, Laos: (6275)	4	6.5–7.2 7.0±0.34	7.3–8.5 7.7±0.59	0.8–0.9 0.9±0.06	44.1–47.1 45.0±1.52	6½

.....continued on the next page

Table 3.1 Shell measurements for populations of the three *Haploptychius*, four *Perrottetia* and one *Indoartemon* species collected (Continued).

Specie and locality and CUMZ nos	No. of specimens	Rangs, mean ± S.D. in mm of:				Number of whorls
		Shell height (H)	Shell width (W)	H/W ration	Shell angle	
Haploptychius blaisei (Dautzenberg and Fischer, 1905)						
10. Tam Phatok, Ngoi District, Luang Phrabang, Laos: (6276, 6277)	16	5.4–6.7 6.2±0.35	9.1–10.5 9.8±0.36	0.5–0.7 0.6±0.05	53.7–75.3 67.1±5.9	6½
Perrottetia aquilonaria Siriboon and Panha, 2013						
12. Ban Namone, Xayabouly District, Xayabouly, Laos (about 40 Km. from Ngeun District, Lao-Thai border to Xayabouly): (6278, 6279)	3	4.1–4.5 4.4±0.19	5.4–6.4 6.0±0.55	0.7–0.9 0.7±0.09	48.4–59.1 54.2±5.43	5½–6
Perrottetia unidentata sp. n.						
13. Ban Nawit, Viengxay District, Houaphane, Laos: (6281, 6282, 6283)	8	4.0–5.8 5.0±0.05	8.9–9.7 9.3±0.25	0.4–0.6 0.5±0.06	67.0–88.9 76.8±6.74	6–6½
14. Tam Than Kaisone Phomvihan, Viengxay District, Houaphane, Laos: (6284, 6285)	5	5.0–6.5 5.9±0.77	7.4–8.2 7.7±0.36	0.6–0.8 0.7±0.11	54.5–60.7 57.1±2.51	6
Perrottetia magnadenta sp. n.						
15. Km 70, Yommarat District, Khammouan, Laos: (6286, 6287)	36	6.0–7.6 6.7±0.36	7.2–8.8 7.8±0.42	0.7–0.9 0.8±0.06	47.4–59.9 54.5±3.34	6
Indoartemon diodonta sp. n.						
16. Tam Xang, Tha Khek District, Khammouan, Laos: (6289, 6290)	49	6.8–8.0 7.4±0.33	6.9–8.6 7.7±0.37	0.8–1.0 0.9±0.06	42.1–58.1 51.8±3.03	6½–7
17. Tam Nang Ann, Tha Khek District, Khammouan, Laos: (6291)	7	7.9–8.9 8.6±0.33	7.2–8.3 7.8±0.34	1.0–0.1 1.1±0.03	46.4–52.4 49.7±2.07	6½–7
18. Tam Xieng Lieb, Tha Khek District, Khammouan, Laos: (6292)	15	6.8–7.8 7.3±0.27	6.4–7.8 7.3±0.46	0.8–1.1 1.0±0.09	41.3–61.0 51.8±5.04	7

Chapter IV

Taxonomic review of the tree snail genus *Amphidromus* Albers, 1850 (Pulmonata: (Camaenidae) in Laos, with description of two new species

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Abstract

The land snail genus *Amphidromus* Albers, 1850 and subgenus *Syndromus* Pilsbry, 1900 (family Camaenidae) in Laos are revised. Fourteen species from various habitats from deciduous forest and limestone areas throughout Laos were confirmed. The classification was revised and discussed based on materials examined from Laos, Cambodia, Vietnam and Thailand compared with the type specimens from many museums. Two new species, *A.* (*Amphidromus*) *syndromoideus* Inkhavilay and Panha sp. nov., from central Laos, and *A.* (*Syndromus*) *xiengkhaungensis* Inkhavilay and Panha sp. nov., from northern Laos, are described and discussed.

Keywords. limestone, *Amphidromus*, classification, systematics, Southeast Asia

Introduction

The Camaenidae family is comprised of some of the most fascinating land snails, and they occur in various habitat types in Southeast Asia. Many genera are ground dwellers but some are considered to be tree dwellers or arboreal snails, including those in the genus *Amphidromus* Albers, 1850. Members of *Amphidromus* have a conical shell (dextral and/ or sinistral) and are very diverse in their shell color and banding patterns (Laidlaw and Solem, 1961; Pilsbry, 1900; Sutcharit and Panha, 2006). Their distribution ranges from Assam in India to Indochina and to Sundaland, south of the Philippines, Wallacea, and a single species found in the Northern Territory of Australia (Pilsbry, 1900; Solem, 1959, 1983). There are about 95 recognized species, which are classified into two subgenera (Thach 2014, 2015; Thach and Huber 2014; Sutcharit et al., 2015 and reference therein; Vermeulen et al., 2015). The nominotypical subgenus usually has a larger shell, is chirally dimorphic and has a long epiphallus and flagellum, whereas the smaller shells of the subgenus *Syndromus* Pilsbry, 1900 is mostly of the sinistral type (except two species, *Amphidromus glaucolarynx* (Dohrn, 1861) is enantiomorphic and *Amphidromus kuehni* Möllendorff, 1902 is dextral) with a short epiphallus and flagellum (Pilsbry 1900; Zilch 1953; Sutcharit and Panha 2006; Sutcharit et al., 2007, 2015).

Most members of the genus *Amphidromus* were named before the 19th century, based exclusively on shell characters, and many of them are known from only a single shell or a few type specimens with rough locality information (Sutcharit *et al.,* 2015). Because *Amphidromus* exhibits a high degree of variation in shell color and banding patterns, its classification is very complicated and problematic. Although several efforts on the taxonomy of *Amphidromus* and the catalogues and illustrations of the type specimens have been provided (Fulton, 1896; Laidlaw and Solem, 1961; Pilsbry, 1900; Sutcharit et al., 2015; Zilch, 1953), the wide range of morphological variation within *Amphidromus* raises doubt as to whether those previous revisionary works may be inapplicable for recent collections, especially since multiple names have been ascribed to single taxa making species recognition confusing.

Laos is located near the center of the Indo-Burmese hotspots (Myers et al., 2000), which has a high diversity of forest types and pristine ecosystems that can potentially support a very high diversity of land snail fauna. Almost all the groups of land snails in Laos are poorly studied compared to in other Indo-China countries. Only six species of *Amphidromus* have been reported so far from Laos: *A. flavus* (Pfeiffer, 1861), *A. xiengensis* Morlet, 1891, *A. haematostoma* Möllendorff, 1898, *A. laosianus* Bavay, 1898, *A. givenchyi* Geret, 1912 and *A. protania* Lehmann and Maassen, 2004, compared to, for example, 19 and 23 species in Thailand and Vietnam, respectively, (Panha, 1996; Schileyko, 2011; Sutcharit et al., 2015). The present study focused on the basic taxonomy of the tree snail genus *Amphidromus* in Laos. The recently collected specimens were investigated together with reference materials in several museum collections. The previous uncertain recorded species and vague status in Laos are re-described based on the type specimens and the genital characters. In addition, we proposed a shell banding system for describing members of the subgenus *Syndromus* and described the informative genitalia and radula characters of this subgenus based on the type species. Lastly, six new records and two new and endemic species are carefully described.

Materials and Methods

The empty shells and living specimens were collected throughout Laos from different elevations above mean sea level (amsl) and forest types and also from fruit orchards. Living specimens were photographed before preserving, initially at -20 ^{o}C and subsequently in 95% (v/v) ethanol, prior to conducting the anatomical study. Genital morphology was critically examined. Intact adult shells were measured for whorl number, shell height (h), and major diameter or shell width (d) using digital Vernier calipers (Mitutoyo, CD-6 CS). The buccal masses were removed and soaked in 10% (w/v) potassium hydroxide solution for 3–5 hours before extracting the radula, and then cleaned in distilled water and preserved in 95% (v/v) ethanol. Radulae were examined by scanning electron microscopy (SEM; JEOL, JSM-5410 LV), recording the formula and shape of the teeth.

Abbreviations

The terms proximal and distal were used for the region closest to and furthest away from the genital orifice, respectively. New abbreviations are introduced for the vaginal stimulator pilaster (vsp) and vaginal pouch (vpo), but all others are as defined by Solem (1983) and Sutcharit and Panha (2006):

ag, albumen gland

ap, appendix

at, atrium

D, dextral

e, epiphallus

fl, flagellum

fo, free oviduct

gd, gametolytic duct

gs, gametolytic sac

hd, hermaphroditic duct

hg, hermaphroditic gland

ov, oviduct

p, penis

pr, penial retractor muscle

S, sinistral

v, vagina

vd, vas deferens

vpo, vaginal pouch

vsp, vaginal stimulator pilaster

Institutional abbreviations

ANSP: The Academy of Natural Science of Philadelphia, Drexel University, Philadelphia.

CUMZ: Chulalongkorn University Museum of Zoology, Bangkok.

MNHN: Muséum national d'histoire naturelle, Paris.d'

NHMUK: The Natural History Museum, London.

RBINS: Royal Belgian Institute of Natural Science, Brussels.

RMNH: Naturalis Biodiversity Center, Rijksmuseum van Natuurlijke Historie, Leiden.

SMF: Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main.

ZMB: Museum für Naturkunde, Berlin.

Systematics

Family Camaenidae Pilsbry, 1895

Genus *Amphidromus* Albers, 1850

Subgenus *Amphidromus* Albers, 1850

Amphidromus Albers, 1850: 138. Martens 1860: 184. Fulton 1896: 66, 94.

Type species. *Helix perversus* Linnaeus, 1758 by the subsequent designation of E. von Martens in Albers (1860).

***Amphidromus* (*Amphidromus*) *roseolabiatus* Fulton, 1896**

Figs 4.1, 4.2A, B, 4.3A, B, 4.4A–F, 4.6A, B, 4.7A–C, Table 4.1

Amphidromus roseolabiatus Fulton, 1896: 89, pl. 6, fig. 8. Type locality: Siam [Thailand]. Pilsbry 1900: 188, pl. 60, fig. 36. Laidlaw and Solem 1961: 527. Richardson 1985: 42. Schileyko 2011: 57. Sutcharit et al., 2015: 88, fig. 13j, k.

Material examined

Lectotype NHMUK 19601462 (Sutcharit et al., 2015: fig. 13j) and paralectotype NHMUK 19601463 (1S shell, Sutcharit et al., 2015: fig. 13k). Ban Phone Can, Yommalat District, Khammouan, Laos: CUMZ 7001 (5D + 3S shells). Wat Paphar, Khamkert District, Bolikhamxay, Laos: CUMZ 7002 (5D + 1S shells). Thad Mouang, Khamkert District, Bolikhamxay, Laos: CUMZ 7003 (2D + 1S shells). Tam Mung Korn, Khamkert District, Bolikhamxay, Laos: CUMZ 7004 (4D + 10S specimens in ethanol; Fig. 4.4E, F), 7005 (13S

specimens in freezer, Fig. 4.2B). Nam Turn Bridge, Khmakert District, Bolikhamxay, Laos: CUMZ 7006 (1D + 1S specimens in ethanol; Fig. 4.4C, D), 7007 (4D + 5S specimens in freezer, Fig. 4.3A, B). Limestone quarry, Bolikhamxay, Laos: CUMZ 4013 (8D + 6S shells). Km. 70 on the road from Laos to Vietnam border, Yommalat District, Khammouan, Laos: CUMZ 7008 (4D + 3S shells, pink aperture). Tam Narng Lod, Yommalat District, Khammouan, Laos: CUMZ 7009 (8D shells, pink aperture). Hauy In River, Yommalat District, Khammouan, Laos: CUMZ 7010 (3D + 1S shells, pink aperture). Ban Pha Vong, Yommalat District, Khammouan, Laos: CUMZ 7011 (12D + 8S specimens in ethanol, pink aperture; Fig. 4.4A, B), 7012 (5D specimens in ethanol, Figs 4.2A, 4.6A, B, 4.7A–C). Thad Khaungsy Waterfall, Luang Phrabang District, Luang Phrabang, Laos: CUMZ 7013 (1D + 1S shells, pink aperture), 7047 (6D specimens in ethanol), 7048 (4D specimens in ethanol), 4035 (1D + 1S shells, pink aperture). Ban Phahom, Vang Vieng District, Vientiane, Laos CUMZ 4017 (6D shells), 7049 (10S + 21D shells). Phong Nha National Park, Vietnam CUMZ 7053 (2D+3S shells). Nan Province, Thailand CUMZ 7054 (1D shell).

Description

Shell chirally dimorphic, elongated to ovated conic, rather thin and glossy. Spire conic; apex acute, light brown and without black spot on the tip. Whorls 6 to 7 nearly smooth; suture wide and depressed; last whorl rounded. Periostracum usually deciduous to yellowish-green radial streaks, more conspicuous on last whorl and faded in previous whorls. Last whorl processes thin, whitish subsutural band, sometimes with one or two reddish-brown spiral bands below periphery but usually not reach to the lip; varix absent. Parietal callus thin and transparent. Aperture ovated to elongated; peristome expanded and not reflected; lip usually purplish-pink or white. Columella straight, thickened with purplish-pink or white. Umbilicus rimate.

Radula

Each row contains about 130 (66-(10-6)-1-(6-10)-63) teeth. Central tooth unicuspid and spatulated with curved cusp. Lateral teeth bicuspid. Endocone cylindrical, slightly oblique, with wide notch; ectocone large with truncated to rounded cusp. Marginal teeth tricuspid start around tooth number 6 to 10; endocone small;

mesocone large with rounded cusp, ectocone small with sharp cusp. Outermost teeth with small and sharp cusp endocone and extocone; mesocone large with curved cusps (Fig. 4.7A–C).

Genital organs

Atrium (at) slightly short (n = 10). Penis (p) long and stout. Epiphallus (e) long, about two times longer than penis; flagellum (fl) longer than epiphallus and terminated in folded coil. Appendix very small, extends from folded coil of flagellum, about same length of epiphallus. Penial retractor muscle (pr) short, thickened and insert distally on penis. Vas deferens (vd) narrow tube connected between epiphallus and free oviduct (Fig. 4.6A).

Internal penial wall corrugated into series of thick penial pilasters (pp), which form a fringe around penial verge. Penial verge (pv) slightly long and curved, conic, smooth surface and orifice located at tip (Fig. 4.6B).

Vagina cylindrical, about two times longer than penis. Gametolytic duct very long, proximal to genital orifice large, coiled; distal to genital orifice tapering to small tube, short about one-third to proximal part and connected to enlarged gametolytic sac. Oviduct and albumin gland small (Fig. 4.6A).

Internally, vaginal wall performs longitudinal vaginal pilasters (vp); proximal to genital orifice, with little corrugated continuous ridges, and distally become smooth ridges (Fig. 4.6B).

Distribution

This species is distributed widely from many localities in the central and northern Laos. There were also records from Nan Province, Thailand and Phong Nha National Park, Vietnam.

Remarks

Amphidromus roseolabiatus differs from *A. smithi* Fulton, 1896 and *A. ventrosulus* Möllendorff, 1900 (Zilch 1953; Sutcharit et al., 2015) in having an enantiomorphic shell coiling, purplish-pink lip and fine green streaks. In contrast, *A.*

smithi has a sinistral shell, brownish lip with dark spot on apex, and *A. ventrosulus* has a sinistral shell, uniform green color, elongated spire and more depressed suture.

Laidlaw and Solem (1961) recognized *A. roseolabiatus* as an uncertain subgenus that was probably close to the subgenus *Syndromus*. However, this species exhibits dimorphic shell coiling with a long flagellum and appendix, which are typical characters of the nominotypical subgenus (Fig. 4.6A). Two color forms were observed in the recent collected materials. The typical color form has a greenish radial streaked periostracum and pinkish apertural lip (Figs 4.2A, 4.4A, B). There are some specimens with the typical color form showing one or two additional reddish-brown lower peripheral bands (Fig. 4. 4B). The second, whitish form usually has a greenish periostracum, as in the typical color form, but a white apertural lip (Figs 4.2B, 4.4C–F). However, these two color forms have identical genital structures and sculptures inside the penis and vagina.

***Amphidromus* (*Amphidromus*) *laosianus* Bavay, 1898**

Figs 4.1, 4.4G

Amphidromus laosianus Bavay, 1898: 15, 16, pl. 2, fig. 1, 1a. Type locality: Khône, sur les bords du Mékong [on the banks of the Mekong River, Khone, Champasak, Laos]. Pilsbry 1900: 183, 184, pl. 62, figs 60, 61. Laidlaw and Solem 1961: 526, 634.

Amphidromus laosianus var. *albocaerulescens* Bavay, 1898: 16, pl. 2, fig. 2, 2a. Type locality: Khône, sur les bords du Mékong [on the banks of the Mekong River, Khone, Champasak, Laos] Pilsbry 1900: 184, pl. 62, figs 62, 63. Laidlaw and Solem 1961: 526, 598.

Material examined

Khone District, Champasak, South Laos: RMNH 101049 (1D + 1S shells, Fig. 4.4G), W.J.M. Maassen collection (1D adult + 2S juveniles). Khone Süd Laos: ZMB Lehmann collection (2D adults + 2D juveniles).

Remarks

Currently known only from the type locality. The unique shell characters are chirally dimorphic, conic to elongated conic; whorls little convex with white subsutural band. Shell color with yellowish-brown or brownish radial streaks on pinkish to whitish ground color; dark varix present. Aperture elongated; peristome thickened, expanded and reflected; lip folded and pinkish. Parietal callus pinkish and thickened; columella pinkish and straight; umbilicus imperforated.

Laidlaw and Solem (1961) mentioned that this species is similar to *A. atricallosus leucoxanthus* variety "*laidlawi*" (Solem 1965: pl. 1, fig. 3; Sutcharit and Panha 2006: fig. 4d, e). However, it differs in having a slender shell and pinkish peristome, parietal callus and inside aperture, while the "var. *laidlawi*" has a white lip, parietal callus and inside aperture, and more depressed suture. Furthermore, *A. cambojiensis* (Reeve, 1860) can be distinguished from this species by having a very large and thickened shell, thickened and white parietal callus and lip, and purplish inside aperture (see Sutcharit et al., 2015).

***Amphidromus* (*Amphidromus*) *pervariabilis* Bavay & Dautzenberg, 1909**

Figs 4.1, 4.5A–L, Table 4.1

Amphidronus pervariabilis Bavay and Dautzenberg, 1909: 246, 247. Type locality: Ban-Lao, Muong-Kong, Pha-Long, Pac Kha. Bavay and Dautzenberg 1909: 279–281, pl. 9, figs 1–10, pl. 10 fig. 1–8. Laidlaw and Solem 1961: 527, 528. Richardson 1985: 15.

Material examined

Syntypes of *A. pervariabilis* s.s. MNHM-IM-2000-2049 (2 shells, Fig. 4.5A, B) from Ban-Lao [19° 39' N, 103° 19' E], Muong-Kong [19° 33' N, 104° 44' E], Pha-Long [22° 48' N, 104° 14' E], Pac Kha [21° 00' N, 104° 35' E]. Syntypes of *A. pervariabilis* var. "*bifasciata*" MNHM-IM-2000-2059 (2 shells, Fig. 4.5C) from Ban-Lao, Muong-Kong, Pha-Long, Pac Kha. Syntype of *A. pervariabilis* var. "*goniostoma*" MNHM-IM-2000-2058 (1 shell, Fig. 4.5D) from Phong-Tho [22° 34' N, 103° 22' E]. Syntypes of *A. pervariabilis* var. "*lilacina*"

MNHM-IM-2000-2052 (2 shells, Fig. 4.5E) from Ban-Lao. Syntype of *A. pervariabilis* var. "*minor*" MNHM-IM-2000-2050 (1 shell, Fig. 4.5F) from unknown locality. Syntypes of *A. pervariabilis* var. "*monozonalis*" MNHM-IM-2000-2057 (2 shells, Fig. 4.5G) from Ban-Lao. Syntype of *A. pervariabilis* var. "*obesa*" MNHM-IM-2000-2053 (1 shell, Fig. 4.5H) from Muong-Bo [22° 24' N, 102° 49' E]. Syntype of *A. pervariabilis* var. "*protracta*" MNHM-IM-2000-2051 (1 shell, Fig. 4.5I) from Ban-Lao, Muong-Kong, Pha-Long, Pac Kha. Syntypes of *A. pervariabilis* var. "*tricolor*" MNHM-IM-2000-2054 (2 shells, Fig. 4.5J) from Ban-Lao.

Km 34, road to Ban Namly, Khua District, Phongsaly, Laos (21° 11' 55.5" N, 102° 6' 40.2" E, 834 m amsl): CUMZ 7014 (3 shells, Fig. 4.5K, L).

Description

Shell chirally dimorphic, elongated conic, rather thick and glossy. Spire elongated conic; apex acute with or without black spot on tip. Whorls 6 to 7 convex to smooth; suture wide and shallow; last whorl rounded to well rounded. Periostracum thin corneous; varix usually absent. Shell color varies from uniform white, yellowish to reddish brown or with narrow to wide brownish peripheral and umbilical bands. Parietal callus thin and transparent. Aperture ovate to oblique elongated; peristome expanded and not reflected; lip white or brownish or purplish. Columella straight, thick or thin and white or brownish. Umbilicus imperforated.

Remarks

This species tended to have a high diversity of shell colors, with eight infra-specific names being provisionally proposed to distinguish the distinct shell shape and color patterns. We examined all the type specimens and recognized them as subspecific entities of one species.

Laidlaw and Solem (1961) recognized this species as a synonym of *A. dautzenbergi* Fulton, 1899. The latter species exhibits a thin shell, yellowish with thin faded greenish streak near umbilicus, white subsutural band and elongated ovate aperture, while, *A. pervariabilis* has a thick shell, monochrome or with dark brown spiral band and ovate aperture. However, the type locality of *A. dautzenbergi* was

"Tonkin", the historical political division during the French colonial period, and is still an uncertain boundary. It known only from the holotype (Sutcharit et al., 2015: fig. 6g), no specimen was found in the present study, and so the taxonomic status between *A. dautzenbergi* and *A. pervariabilis* remains to be confirmed.

***Amphidromus* (*Amphidromus*) *givenchyi* Geret, 1912**

Figs 4.1, 4.2C, 4.3C, 4.4I, Table 4.1

Amphidromus givenchyi Geret, 1912: 55, 56, pl. 2, figs 21, 22. Type locality: Unknown. Laidlaw and Solem 1961: 526, 621. Richardson, 1985: 43. Sutcharit and Panha 2006: 26–28, figs 4n–q, 18, 19.

Material examined

Thad Lor Waterfall, Salavan District, Salavan, Laos: CUMZ 7015 (120D adult shells + 18D juvenile shells; Figs 4.3C, 4. 4I), 7016 (7D specimens in ethanol; Fig. 4.2C). Wat Phou (Temple on the mountain), Khong Xédon District, Salavan, Laos: CUMZ 7017 (61D adult shells + 8D juvenile shells), 7018 (2D specimens in ethanol).

Remarks

The species description, genitalia and radula morphology have been carefully described in Sutcharit and Panha (2006), which allows an unambiguous recognition for this species. The unique characters are a relatively medium sized (compared to other members of this genus shown in Table 4. 1), ovate-conic and dextral shell. Apex with black spot. Aperture oblique; peristome expanded and not reflected. Parietal callus thin and transparent to slightly thickened and white. Shell color uniform greenish with pale to yellowish color on earlier whorl, and greenish subsutural band. Genitalia contains long and slender penis, short and curved epiphallus of equal length to flagellum; proximal to enlarged and coiled appendix epiphallus; appendix short.

The early records of this species were from the Ubon Ratchathani and Kalasin Provinces of Thailand, and the Luang Phrabang and Savannakhet Provinces of Laos (Sutcharit and Panha 2006). Here, two more localities from Salavan Province, Laos were added. All of the records are from dry dipterocarp to deciduous forests with sandstone

hills. The snails were found in small holes on branch or tree trunk during the aestivation period (Fig. 4.3C).

***Amphidromus* (*Amphidromus*) *protania* Lehmann & Maassen, 2004**

Figs 4.1, 4.4H

Amphidromus (*Amphidromus*) *protania* Lehmann and Maassen, 2004: 17–20, figs 1–4.

Type locality: South Laos, Salavan Province, near the Ban Donxé Village, the east bank of the Se Don River.

Material examined

Holotype RMNH 98143 (Fig. 4.4H), paratypes RMNH 98144 (4D shells).

Remarks

No specimen was found in this recent survey. *Amphidromus protania* has a very similar shell shape to the dipterocarp forest species *A. givenchyi*. The genitalia contains a long and coiled proximal part of epiphallus with a relatively short appendix, as in *A. givenchyi* (Lehmann and Maassen 2004; Sutcharit and Panha 2006). However, the distinguishing characters from *A. givenchyi* are the relatively smaller shell (height 26–31 mm in *A. protania*; Table 4. 1), yellowish shell color, and brownish subsutural and spiral bands on the periphery. Moreover, Lehmann and Maassen (2004) mentioned that the brownish banding pattern had less variation. However, a brownish spiral band on the periphery can also be observed in juvenile *A. givenchyi* (see Sutcharit and Panha 2006: fig. 4o). Moreover, this species occurs in dipterocarp forest within the range of *A. givenchyi*, therefore, it is possibly a shell color variant of *A. givenchyi*. Additional specimens for further anatomical and molecular evidences are desirable to test this hypothesis.

***Amphidromus* (*Amphidromus*) *syndromoideus* Inkhavilay & Panha sp. nov.**

Figs 4.1, 4.2D, 4.3D, 4.4J, K, 4.6C, D, 4.7D–F, Table 4.1

Etymology

The specific name "*syndromoideus*" is from "*syndromus*", an *Amphidromus* subgeneric name and suffice "*–oideus*" meaning "like or resembling". This name refers to the shell morphology resemblance of the new species with members of the subgenus *Syndromus*.

Type material examined

Holotype CUMZ 7019 (Figs 4.2D, 4.3D, 4.4J, 4.6C, D, 4.7D–F). Measurement: shell height 28.2 mm, shell width 13.4 mm and 6½ whorls.

Paratypes CUMZ 7020 (22D + 9S shells; Fig. 4.4K, Table 4. 1), CUMZ 7021 (1S specimen in ethanol), NHMUK (1D + 1S shells), SMF (1D + 1S shells).

Type locality. Tam Nang Ann (cave), Thakhek District, Khammouan, Laos (17° 26' 39.2" N, 104° 56' 54.8" E), and 163 m amsl.

Diagnosis

The new species differs from all other known *Amphidromus* (*Syndromus*) species in having a long epiphallus and flagellum, and very long appendix, which are unique characters of the nominotypical subgenus (Solem 1983; Sutcharit and Panha 2006). The new species differs from *A. roseolabiatus* in having a small and thin shell, inconspicuous greenish radial streaks and about two times longer appendix. While, *A. roseolabiatus* has a larger solid shell, conspicuously greenish radial streaks in fresh specimens, sometimes with a single brownish spiral band below the periphery, purplish-pink apertural lip, and short appendix.

Description

Shell chirally dimorphic, thin, rather small, elongate conic and glossy. Spire conic; apex acute, brownish and without black spot on the tip. Whorls 5 to 6 little convex; suture depressed; last whorl rounded. Periostracum thin and transparent. Last whorl with narrow white subsutural band and shell color uniform yellowish with green

radial streaks on last whorl (pale to inconspicuous in older whorls and empty shells); varix absent. Parietal callus thin and transparent. Aperture wide ovated; peristome little expanded; lip whitish or transparent. Columella straight, thickened and white. Umbilicus rimated.

Radula

Each row contains about 105 (54-(3-5)-1-(3-5)-50) teeth. Central tooth small, unicuspid and spatulo-truncated cusp. Lateral teeth bicuspid; endocone cylindrical with wide notch; ectocone large with truncated cusp. Marginal teeth tricuspid, starting around tooth number 3 to 5; endocone small with sharp cusp; mesocone large with truncated cusp; ectocone smallest. Outermost teeth with curved and pointed cusp of endocone; mesocone large with curved cusp; ectocone triangular shape with pointed cusp (Fig. 4.7D–F).

Genital organs

Atrium (at) slightly short (n = 10). Penis (p) short and conic shaped. Epiphallus (e) long, slender and two times longer than penis. Flagellum (fl) short, about half of epiphallus length and terminated in folded coil. Appendix very long, small tube extends from folded coil of flagellum, about three times longer than epiphallus. Penial retractor muscle (pr) short, thickened and inserted distally on penis. Vas deferens (vd) narrow tube connected between epiphallus and free oviduct (Fig. 4.6C).

Internal penial wall, proximal to genital orifice corrugated into series of thick penial pilasters (pp) form fringe; distal to genital orifice smooth around penial verge. Penial verge (pv) small, conic and smooth surfaced (Fig. 4.6D).

Vagina cylindrical, about four times longer than penis. Gametolytic duct very long, proximal to genital orifice large, coiled; distal to genital orifice tapering to small tube and connected to ovated gametolytic sac. Oviduct and albumin gland very small (Fig. 4.6C).

Internally, vaginal wall shows longitudinal vaginal pilasters (vp); proximal to genital orifice, with smooth, thickened and continuous ridges, and distally pilasters thinner and smooth ridges (Fig. 4.6D).

Distribution

This new species is currently known only from the type locality, a dry evergreen forest with limestone outcrops in the central part of Laos at Thakhek District, Khammouan Province.

Remarks

Two living snails were found during the aestivation period in a small tree hole at 5 m height (Fig. 4.3D).

Subgenus *Syndromus* Pilsbry, 1900

Amphidromus (*Syndromus*) Pilsbry, 1900: 184.

Type species. *Helix contraria* Müller, 1774 by the subsequent designation of Zilch (1960: 623).

Diagnosis

Shell usually sinistral, conic to elongated conic and rather small (height 25 to 40 mm), varices absent and varies in color pattern. Genital characteristics show camaenid type with short epiphallus and flagellum, appendix wanting, vaginal pouch and vaginal stimulator pilaster sometimes present. Radula teeth with spatulated shape.

The subgenus *Syndromus* was firstly nominated as "Sinistral Division" for *Amphidromus* with a relatively smaller sinistral coiling shell (Pilsbry 1900). So far, the genital characters of the type species have never been examined, only Wiegmann (1894) briefly reported the radular and jaw structures of the type species. To clarify the genitalia and radula characters of the subgenus, spirit preserved specimens in the Zoological Museum of Amsterdam (ZMA) collection were examined and are described below:

***Amphidromus* (*Syndromus*) *contrarius* (Müller, 1774)**

Fig. 4.8A, B, E–G

Helix contraria Müller, 1774: 95. Type locality: Unknown.

Amphidromus contrarius—Wiegmann 1894: 208–210, pl. 15, figs 12–17. Fulton 1896: 77, 78. Pilsbry 1900: 210–212, pl. 65, figs 22–27. Haniel 1921: 1–88, pls 1–5. Zilch 1960: 623, fig. 2183. Laidlaw and Solem 1961: 570, 612.

Material examined

ZMA collection from Niki Niki, Central Timor, collected by M. E. Walsh, March-April, 1929 [Niki Niki, Central Amanuban District, South Timor Tengah Regency, East Nusa Tenggara Province, Indonesia].

Shell. Shell morphology was completely described in Pilsbry (1900: 212, 213).

Radula

Teeth arranged in V-shape rows, each row contains about 170 (83-(11-14)-1-(12-14)-86) teeth. Central tooth unicuspid with spatulated shape. Lateral teeth bicuspid, endocone small, ectocone large with truncated cusps, gradually transformed to tricuspid marginal teeth from about tooth number 11 to 14 outwards. Marginal teeth tricuspid, endocone curved shape, mesocone largest with long and obtused cusp, and ectocone smallest with pointed cusp (Fig. 4.8E–G).

Genital organs

Atrium (at) long conic (n = 3). Penis (p) short and swollen distally. Epiphallus (e) about two times longer than penis; flagellum (fl) very short and smaller than epiphallus. Appendix absent. Penial retractor muscle (pr) thin and long. Vas deferens (vd) narrow tube extending from the end of epiphallus to free oviduct (Fig. 4.8A).

Internal penial wall, proximal to genital orifice corrugated with obliquely penial pilasters (pp) form fringe around penial verge; distal to genital orifice smooth. Penial verge (pv) enlarged, elongated, elliptical and smooth surface (Fig. 4.8B).

Vagina (v) short cylindrical, about same length as penis and proximal to genital orifice little swollen; vaginal pouch (vpo) present. Gametolytic duct (gd) long, cylindrical, almost same diameter to vagina; distally tapering to small tube and

connected to spherical gametolytic sac (gs). Free oviduct (fo) short; oviduct (ov) and albumin gland very small (Fig. 4.8A).

Internally, vaginal wall possesses slightly smooth longitudinal pilasters (vp); distally showing weak crenulation pilasters to smooth surface. Vaginal stimulator pilaster (vsp) locates close to atrium with swollen and curled shape (Fig. 4.8B, C).

Remarks

Approximately 45 species are currently recognized in this subgenus. Laidlaw and Solem (1961) divided those recognized species into six supraspecific groups using geographic distribution. All of the Indochina forms (six species) were assembled into the *A. xiengensis* group (Group XIV). However, all the members exhibit diverse shell color patterns. Their genital characters have not yet been described. Here, we attempted to clarify those described specific entities and color forms with distinct reproductive characters and shell banding pattern.

Most of the subgenus *Syndromus* species exhibit diverse shell banding, which can be characterized in terms of five banding systems. The definitions of those five bands and description of shell color forms follow the conventional procedures used in *Euhadra* (Pilsbry 1928), *Cepaea* (Cain and Sheppard 1950; Cain and Currey 1963), *Partula* (Murray and Clarke 1966) *Theba pisana* (see Cowie 1984) and *Satsuma* (Wu et al., 2008). The syndromid species complex maintains a polymorphic color pattern of varied width, shape and coloration. We simplified the banding pattern systems by modifying from that above and dividing them into six sections or six banding systems (Fig. 4.8D), starting from the uppermost of the last whorl to the lowermost near the umbilicus. They are:

Band 1 (subsutural band) just below or contact with the suture, usually thin and sometimes omitted in some species or populations.

Bands 2 and 3 (supra-peripheral bands) begin from below Band 1 to the posterior angle of aperture. These two bands are usually separated with a narrow gap in the middle. Band 2 is located just below Band 1, and Band 3 is placed

above the posterior angle of the aperture. These two bands are usually modified as dotted, blotched or divided into several thinner bands.

Bands 4 and 5 (sub-peripheral bands) locate below the posterior angle of the aperture or below the periphery to the umbilicus. These two bands are usually separated by a narrow to wide gap of ground color. Band 4 normally contacts at the bottom of Band 3. Band 5 locates just around the umbilicus.

Band 6 usually covers the entire umbilical area between the umbilicus and Band 5.

***Amphidromus* (*Syndromus*) *areolatus* (Pfeiffer, 1861)**

Figs 4.1, 4.7G–I, 4.9A, 4.10A–C, 4.12A, B, Table 4.1

Bulimus areolatus Pfeiffer, 1861a: 194. Type locality: Siam [Thailand]. Pfeiffer 1861b: 172, pl. 46, figs 11, 12.

Amphidromus areolatus—Fulton 1896: 81. Pilsbry 1900: 198, 199, pl. 63, figs 85, 86. Laidlaw and Solem 1961: 564. Solem 1965: 624, 625, pl. 1, figs 4–7. Sutcharit et al., 2015: 58, fig. 3j, k.

Material examined

Lectotype NHMUK 19601430 (Sutcharit et al., 2015: fig. 3j), paralectotype NHMUK 19601431 (1 shell). Thad Fek, Sammakeexay District, Attapeu, Laos: CUMZ 7022 (20 shells; Fig. 4.10A–C), 7023 (17 specimens in freezer; Figs 4.7G–I, 4.9A, 4.12A, B). Thad Pha Soam, Paksong District, Champasak, Laos: CUMZ 7024 (8 shells).

Description

Shell sinistral, elongated conic, rather small, thin and glossy. Spire conic; apex acute with black spot on the tip. Whorls 5 to 6 slightly convex; suture depressed; last whorl rounded. Periostracum transparent to thin corneous. Last whorl process yellow to absent Band 1; Bands 2 to 4 (sometimes Bands 2 to 5) usually merge and become brownish slanted blotches with flame shape; Band 6 yellowish or roseate. Parietal callus thin and transparent. Aperture auriform; peristome expanded to little expanded; lip white to transparent. Columella straight and white. Umbilicus rimate.

Radula

Teeth arranged in V-shape rows, each row contains about 126 (62-(13-9)-1-(9-13)-63) teeth. Central tooth tricuspid with triangular shaped mesocone, ectocones very small with pointed cusp. Lateral teeth bicuspid, endocone small with curved cusp; ectocone large with truncated or curved cusps, gradually transformed to tricuspid marginal teeth. Tricuspid marginal teeth start around tooth number 9 to 13 outwards; endocone curved shaped; mesocone largest size with long and obtuse cusp; ectocone smallest with pointed cusp. Outermost teeth with small serrated shape endocone and extocone; mesocone large with curved cusps (Fig. 4.7G–I).

Genital organs

Atrium (at) slightly long (n = 10). Penis (p) long cylindrical and enlarged. Epiphallus (e) short about same length of penis; flagellum (fl) short and terminated pointed tip. Appendix absent. Penial retractor muscle (pr) thin and relatively long. Vas deferens (vd) narrow tube connected between epiphallus and free oviduct (Fig. 4.12A).

Internal penial wall nearly smooth and corrugated into thin penial pilasters, which form fringe around penial verge. Penial verge slightly small, conic and smooth surface (Fig. 4.12B).

Vagina cylindrical, about same length as penis. Gametolytic duct long, proximal to genital orifice, larger diameter than vagina and coiled; distal to genital orifice tapering to small tube about same length with proximal part and connected to gametolytic sac. Oviduct and albumin gland very small (Fig. 4.12A).

Internal wall of vagina shows longitudinal vaginal pilasters (vp); proximal to genital orifice, with nearly smooth surface about half of its length, and distally pilasters become corrugated ridges (Fig. 4.12B).

Distribution

The species is known from southern Laos, where the specimens were collected at Thad Fek, Sammakeexay District, Attapue and Thad Pha Soam, Paksong District, Champasak, Laos in a dry dipterocarp forest.

Remarks

This species can be distinguished from *A. zebrinus* (Pfeiffer, 1861) and *A. begini* (Morlet, 1886) by having a smooth shell surface, brownish spiral Bands 4 and 5 present with white lip. While, *A. zebrinus* (see Sutcharit et al., 2015: fig. 15k) has an elongated conic shape shell, Band 1 absent, and Bands 2 to 5 merged and become slanted radial streaks, and reddish band between Bands 5 and 6. *A. begini* exhibits strong radial ridges, Bands 2 to 6 merged and become slanted brownish radial streaks, and brownish ribs (Fig. 4.10D, syntype MNHN-IM-2000-1832).

***Amphidromus* (*Syndromus*) *flavus* (Pfeiffer, 1861)**

Figs 4.1, 4.9B, 4.10E–K, 4.12C, D, 4.14A–C, Table 4.1

Bulimus flavus Pfeiffer, 1861a: 194. Type locality: Siam [Thailand]. Pfeiffer 1861b: 171, pl. 46, figs 7, 8. Morelet 1875: 265.

Amphidromus flavus—Fulton, 1896: 81. Ancey 1898: 134; Pilsbry 1900: 197, 198, pl. 63 figs 92, 93. Laidlaw and Solem 1961: 563, 564, 619.

Amphidromus flavus var. *proxima* Fulton, 1896: 81; pl. 6, fig. 4. Type locality: Unknown. Sutcharit et al., 2015: 85, fig. 13c.

Amphidromus xiengensis var. *proxima*—Pilsbry 1900: 198, pl. 63, fig. 94. Laidlaw and Solem 1961: 565, 652.

Amphidromus xiengensis var. *tryoni* Pilsbry, 1900: 196, 197, pl. 63, fig. 78. Type locality: Laos Mountains, Cambodia.

Amphidromus sinensis var. *indistinctus* Pilsbry, 1900: 192, pl. 62, fig. 70. Type locality: Laos Mountains.

Material examined

Lectotype NHMUK 19601436 (Sutcharit et al., 2015: fig. 7i), paralectotype NHMUK 19601437 (1 shell). Holotype of var. "*proxima*" Fulton, 1896 NHMUK 1896.6.13.48 (Sutcharit et al., 2015: fig. 13c). Holotype of var. "*indistinctus*" Pilsbry, 1900 ANSP 31486 (Fig. 4.10H). Lectotype of var. "*tryoni*" Pilsbry, 1900 ANSP 31488 (Fig. 4.10I) and paralectoypes ANSP 252745 (2 shells, Fig. 4.10J).

Park at the temple mountain, Luang Phrabang, Laos: NHMUK ex. Brandt collection No. 17320 (5 shells). Tempelberg [Temple Mount], Luang Phrabang, Laos: ZMB ex. Lehmann collection (20 shells). Wat Phousy (Temple), Luang Phrabang, Laos: CUMZ 7025 (33 shells). Ban Na Deauy, Luang Phrabang District, Luang Phrabang, Laos: CUMZ 7026 (3 shells; Fig. 4.10K), 7027 (7 specimens in ethanol; Figs 4.9B, 4.12C, D, 4.14A–C). Mouhot's Tomb, east bank of Kan River, Luang Phrabang District, Luang Phrabang, Laos: CUMZ 7028 (5 shells). Tam Pou Kham, Vang Vieng District, Vientiane, Laos: CUMZ 7029 (16 shells; Fig. 4.10E–G).

Description

Shell sinistral, small, ovated conic, small, thin and glossy. Spire conic; apex acute yellowish with black spot on the tip. Whorls 5 to 6 convex; suture depressed; last whorl rounded to well rounded. Periostracum transparent to thin corneous. Last whorl processes uniform yellowish; Bands 1 to 3 usually absent; Bands 4 and 5 absent or present with indistinct bands; Band 6 usually absent or sometimes present as scantly reddish band. Parietal callus thin and transparent. Aperture ovate to sub-ovate; peristome little thickened and shortly expanded; lip whitish. Columella straight and white. Umbilicus opened to rimed.

Radula

Teeth arranged in V-shape rows, each row contains about 166 (84-(7-10)-1-(8-12)-81) teeth. Central tooth tricuspid; mesocone triangular shape; ectocones small with pointed cusp. Lateral teeth tricuspid; endocone small and rounded cusps; mesocone large and truncated cusp; ectocone very small, pointed cusp and located at base of teeth. Lateral teeth gradually transformed to elongated marginal teeth. Marginal teeth tricuspid starts around teeth number 8 to 12; endocone elongated with dull cusps and separated from mesocome with wide notch; mesocone lartge, elongated and curved cusps; ectocone small with pointed cusps or sometimes serrated shape (Fig. 4.14A–C).

Genital organs

Atrium (at) slightly long (n = 5). Penis (p) long, cylindrical and enlarged from middle to end. Epiphallus (e) cylindrical, length longer than penis; flagellum (fl) short and four-fold shorter than epiphallus; appendix absent. Penial retractor muscle (pr) thickened and relatively short. Vas deferens (vd) small tube, connected between epiphallus and free oviduct (Fig. 4.12C).

Internal penial wall corrugated into thin penial pilasters, which form fringe around penial verge. Penial verge conic, smooth surface and orifice open near the tip (Fig. 4.12D).

Vagina cylindrical, long slender about two times longer than penis length. Gametolytic duct long, proximal to genital orifice almost the same diameter of vagina, distally tapering; distal to genital orifice small tube about same length with proximal part and connected to gametolytic sac. Oviduct and albumin gland small (Fig. 4.12C).

Internally, vaginal wall shows longitudinal vaginal pilasters (vp); pilasters very narrow and thin (Fig. 4.12D).

Distribution

The distribution range of the species is from Vientiane to Luang Phrabang Provinces.

Remarks

Amphidromus flavus differs from *A. sinensis* (Benson, 1851) in having a smaller shell, more spire ovated conic, with a single reddish band on the penultimate whorl, and can be distinguished from *A. xiengensis* by having a smaller shell, ovated conic, without any band on yellowish ground color or on shell sculpture. It differs from *A. globonevilli* Sutcharit and Panha, 2015 by having a larger shell size, and smaller than *A. principalis* Sutcharit and Panha, 2015. In comparison, *A. globonevilli* has an elongated conic shell and with a faint yellow spiral band below the periphery, while *A. principalis* has a more elongated conic shell, last whorl without any band, aperture ovated. In our collection we found two types as *A. flavus* and *A. flavus* var. "*proxima*" living sympatrically at Luang Phrabang and Vang Vieng.

Three subspecific entities have been proposed, however, we recognized them as a single biological species, *A. flavus*.

1. Typical form: monochrome yellowish shell and Bands 1 to 6 absent (Sutcharit et al., 2015: fig. 7i, j, for the lectotype and paralectotype).
2. var. "*proxima*" Fulton, 1896: monochrome yellowish shell, Bands 4 and 5 are indistinct pale brownish bands (Sutcharit et al., 2015: fig. 13c, for the holotype).
3. var. "*tryoni*" Pilsbry, 1900: Band 1 yellowish, Bands 2 and 3 absent, Bands 4 and 5 brownish and Band 6 absent. In some specimens, brownish blotches of Bands 2 and 3 present in the earlier whorls and disappeared in penultimate and last whorls (Fig. 4.10I–K).
4. var. "*indistinctus*" Pilsbry, 1900: identical to the var. "*proxima* Fulton, 1896" (Fig. 4.10H).

Amphidromus* (*Syndromus*) *roemeri (Pfeiffer, 1863)

Bulimus römeri Pfeiffer, 1863a [1862]: 274, pl. 36, fig. 4. Type locality: Laos Mountains, Camboja. Pfeiffer 1863b [1860–1866]: 217, pl. 57, figs 10, 11.

Amphidromus roemeri—Fulton 1896: 80. Pilsbry 1900: 192, 193, pl. 63, figs 95, 96. Laidlaw and Solem 1961: 654. Sutcharit et al., 2015: 87, fig. 13e, f.

Material examined

Lectotype NHMUK 19601450 (Sutcharit et al., 2015: fig. 13e), paralectotype NHMUK 19601451 (1 shell).

Remarks

The type specimens have recently been figured in Sutcharit et al., (2015: fig. 13e, f). The unique characters of this species are the sinistral, ovated conic shell; spire brownish color; last whorl well rounded. Shell whitish ground color, Bands 1 to 3 and 6 absent and Bands 4 and 5 perform reddish brown bands. Aperture ovate; peristome little expanded; lip white.

Amphidromus roemeri was described based on specimens collected by H. Mouhot with the type locality from "Laos Mountains, Camboja". This collection locality is a historical geographic name with an uncertain boundary. So far, this species is known only from the type specimens and an uncertain record from Laos by Laidlaw and Solem (1960: 654). However, no specimens were found in the present study, therefore the records from Laos still remain to be confirmed.

Laidlaw and Solem (1961) placed *A. roemeri* as a junior synonym of *A. sinensis* (Benson, 1851) from south of China. We have examined the type specimens of both species and found that *A. roemeri* (see Sutcharit et al., 2015: fig. 13e, f) differs from *A. sinensis* by having an ovated conic, whitish shell, aperture ovate, spire short conic, last whorl well rounded. While, *A. sinensis* (see Sutcharit et al., 2015: fig. 16g–i) has a yellowish shell, elongated conic spire, aperture auriform and last whorl rounded. Furthermore, *A. globonevilli* differs by having a larger shell, spired conic, yellowish shell and aperture oblique.

***Amphidromus (Syndromus) semitessellatus* (Morlet, 1884)**

Fig. 4.10L, M

Bulimus (Amphidromus) semitessellatus Morlet, 1884: 387, 388, pl. 11, figs 2, 2a. Type locality: Les montagnes qui bordent le grand fleuve au delà de Stung-Treng. Les forêts et les montagnes de Kampot a Campong-Som [Mountains and forest in Stung Treng, Kampot and Sihanoukville Provinces, Cambodia]. Fischer-Piette 1950: 153.

Amphidromus semitessellatus—Morlet 1889: 128. Fulton 1896: 87. Pilsbry 1900: 194, pl. 60, figs 41–44. Laidlaw and Solem 1961: 564. Solem 1965: 625, 626, pl. 2, fig. 2. Richardson 1985: 43.

Material examined

This species was described from specimens collected by M. Pavie from the L. Morlet collection. The original description includes an illustration of a single shell, one set of shell measurements, and the species description that may be based on one

unknown specimen. There is a single specimen of L. Morlet in the MNHN collections with an original label stating “Type”. Fischer-Piette (1950: 153) wrote the “holotype, 35 mm” which we considered to be an inadvertent lectotype designation (ICZN 1999: Art. 74.5). Therefore, lectotype MNHN-IM-2000-1985 (Fig. 4.10L) was designated by Fischer-Piette (1950: 153) to stabilise the name.

Cambodia: RBINS Dautzenberg collection (3 shells). NHMUK (1 juvenile, Fig. 4.10M).

Remarks

Shell sinistral, elongated conic, thickened and glossy. Spire conic; apex acute with brown or black spot on the tip. Whorls 6 to 7 slightly convex; suture depressed; last whorl rounded. Periostracum thin. Last whorl monochrome whitish with black Band 1 and Bands 2 to 6 absent; spire with concurrent brownish blotches of Bands 2 and 3. Parietal callus thickened and transparent or white. Aperture sub-ovated; peristome rather thickened expanded and little reflected; lip whitish. Columella thickened, perpendicular and white. Umbilicus rimate to perforate.

Previous records of this species were from the type locality in Stung Treng Province in the north and Kampot and Sihanoukville Provinces in the south of Cambodia, and later from Srakeo Province, Thailand. Laidlaw and Solem (1961: 658) mentioned that the distribution range of this species was in Laos. However, no specimens were collected and so new records of this species in Laos are required to confirm its precise distribution.

Amphidromus semitessellatus can be distinguished from *A. flavus* and *A. xiengensis* in having a solid shell, with black Band 1, last whorl monochrome whitish, Bands 2 to 6 absent, and spire with concurrent brownish blotches of Bands 2 and 3. In comparison, *A. flavus* has a yellowish and thin shell, Bands 1 to 6 usually absent, but sometimes Bands 4 and 5 present and with scantly reddish Band 6. While, *A. xiengensis* exhibits a yellowish ground color, thinner shell, reddish Band 1, Bands 2 and 3 with concurrent brownish slanted blotches, dark brown Bands 4 and 5, and yellowish or reddish Band 6.

Similar to the previous species, color variation occurs in this species in having concurrent brownish blotches of Bands 2 and 3 on first half of last whorl and blackish spiral Bands 4 and 5 present, but do not continue to the lip, and black Band 6.

***Amphidromus* (*Syndromus*) *xiengensis* Morlet, 1891**

Figs 4.1, 4.9C, D, 4.11A–H, 4.13A, B, 4.14D–F, Table 4.1

Amphidromus xiengensis Morlet, 1891a: 27. Type locality: Xieng-Mai et les forets des bords du Ménam Pinh, Laos occidental [banks of Ping River, Chiang Mai Province, Thailand]. Morlet 1891b: 232, 240, 241, pl. 5, fig. 4. Ancey 1898: 134. Pilsbry 1900: 194-195, pl. 63, figs 75, 76. Fischer-Piette 1950: 159. Laidlaw and Solem 1961: 564, 565. Solem 1965: 626, 627, pl. 2, figs 7-13.

Amphidromus porcellanus var. *xiengensis*—Fulton 1896: 79.

Amphidromus contrarius var. *multifasciata* Fulton, 1896: 78, pl. 7, fig. 5. Type locality: Cambodia.

Amphidromus xiengensis var. *multifasciatus*—Pilsbry 1900: 195, pl. 63, fig. 77. Solem 1965: 626.

Amphidromus xiengensis var. *clausus* Pilsbry, 1900: 195, 196, pl. 63, figs 79–82. Type locality: Laos Mountain, Cambodia. Solem 1965: 626, pl. 2, figs 11-13.

Material examined

The species was described based on material from Muséum ex. M. Pavie collection and did not include an illustration. Morlet (1891b: 240, 241, pl. 5, fig. 4) subsequently re-published the description and illustrated a single specimen. There is a single specimen of L. Morlet in the MNHN collection with an original label stating "Type". Fischer-Piette (1950: 159) wrote the "holotype, 38 mm" which we considered to be an inadvertent lectotype designation (ICZN 1999: Art. 74.5). Therefore, lectotype MNHN-IM-130306224 (Fig. 4.8A) was designated by Fischer-Piette (1950: 153) to stabilise the name.

Lectotype of var. "*multifasciata*" Fulton, 1896 NHMUK 19601458 (Sutcharit et al., 2015: fig. 11f), paralectotypes NHMUK 19601459 (2 shells). Lectotype of var.

"*clausus*" Pilsbry, 1900 ANSP 31496 (Fig. 4.11D) and paralectotypes ANSP 252752 (2 shells).

Xieng-Moi (Laos occidental): NHMUK 1893.12.8.40 ex. Dautzenberg collection (1 shell). Lao Moutains, Cambodia: NHMUK 19601539 ex. Cuming collection (3 shells). Ban Phon Pai, Bachieng District, Champasak, Laos: CUMZ 7030 (32 shells). Thad Pha Soam, Boloven Plateau, Paksong District, Champasak, Laos: CUMZ 7031 (9 shells). Ban Oudom, Pakbeng District, Oudomxay, Laos: CUMZ 7032 (6 shells). Mouhot's tomb, east bank of Kan River, Luang Phrabang District, Luang Phrabang, Laos: CUMZ 7033 (7 shells). Thailand: CUMZ 7050 (1 shell; Fig. 4.11B). Tam Chiang Dao, Chiang Dao District, Chiang Mai, Thailand: CUMZ 7034 (1 shell; Fig. 4.11C). Thad Kacham water fall, Luang Phrabang District, Luang Phrabang, Laos CUMZ 7035 (2 specimens in ethanol; Figs 4.9C, D, 4.13A, B). Ban Na Deauy, Luang Phrabang District, Luang Phrabang, Laos: CUMZ 7036 (4 shells; Fig. 4.11E), 7037 (2 specimens in ethanol; Fig. 4.14D–F). Pha Tang, Chiang Mai, Thailand CUMZ 7052 (1 shell; Fig. 4.11F). Doi Phou Nang National Park, Chiangmouan, Phayao, Thailand: CUMZ 7038 (3 shells; Fig. 4.11G, H). Thad Khaungsy Waterfall, Luang Phrabang District, Luang Phrabang, Laos: CUMZ 7039 (1 specimen in ethanol).

Description

Shell sinistral, conic to elongated conic, rather thick and glossy. Spire conic; apex acuted with brown or black spot on the tip. Whorls 6 to 7 slightly convex; suture depressed; last whorl rounded. Periostracum thin and corneous. Last whorl with reddish to brown Band 1; Bands 2 and 3 as concurrent slanted brownish blotches continuous to expanded lip; Bands 4 and 5 with brownish spiral bands; Band 6 absent or yellowish to reddish. Parietal callus transparent or little thickened and white. Aperture sub-ovate; peristome rather thick and expanded; lip whitish. Columella thickened, perpendicular and white. Umbilicus rimed to perforated.

Radula

Each row contains about 157 (79-(21-17)-1-(17-21)-77) teeth. Central tooth monocuspid and spatulated shape. Lateral teeth bicuspid; endocone elongated shape, curved cusp and separated from truncated or curved cusps of ectocone with wide

notch, teeth gradually transformed to tricuspid marginal teeth. Marginal teeth tricuspid start around teeth number 17 to 21 outwards; endocone curved and pointed cusps; mesocone large with truncate or obtused cusps; ectocone small, triangular shape with pointed cusp. Outermost teeth with pointed cusps endocone; mesocone large with curved cusps; extocone sometime with serrated shape (Fig. 4.14D–F).

Genital organs

Atrium (at) slightly short (n = 5). Penis (p) long, cylindrical and enlarged at middle. Epiphallus (e) cylindrical, two-fold longer than penis; flagellum (fl) short, three-fold shorter than epiphallus; appendix absent. Penial retractor muscle (pr) thickened and relatively short. Vas deferens (vd) small tube, connected between epiphallus and free oviduct (Fig. 4.13A).

Internal penial wall corrugated into weak penial pilasters, which form fringe around penial verge. Penial verge conic, rough surface and orifice open near the tip (Fig. 4.13B).

Vagina cylindrical, long slender about 1.5 times longer than penis. Gametolytic duct long, proximal to genital orifice the same diameter of vagina and distally tapering; distal to genital orifice very small tube about same length as proximal part and connected to gametolytic sac. Oviduct and albumin gland very large (Fig. 4. 13A).

Internal wall of vagina shows longitudinal vaginal pilasters (vp); pilasters vary narrow and thin throughout vaginal length (Fig. 4.13B).

Distribution

The species is widely distributed, and can be found in several habitats, such as forests, fruit orchards and limestone areas between latitudes 14–16 N.

Remarks

Amphidromus xiengensis differs from *A. areolatus* and *A. zebrinus* in having a larger shell, reddish Band 1, concurrent slanted and brownish blotched Bands 2 and 3, and brownish spiral Bands 4 and 5, whereas, the other two species have a smaller shell, Band 1 absent and Bands 2 and 3 merged and become brownish slanted

blotches in *A. zebrinus* or brownish slanted blotches with a flame shape in *A. areolatus*. It differs from *A. eudeli* Ancey, 1897 (Fig. 4. 11N, syntype RBINS 617427) and *A. fuscolabris* Möllendorff, 1898 (Fig. 4.11I, holotype SMF 7641) in having a white peristome, reddish Band 1, and Bands 2 and 3 usually separated. In comparison, *A. fuscolabris* shows a purplish-pink peristome, yellowish Band 1, Bands 2 to 5 merged and roseated Band 6, while, *A. eudeli* exhibits a brownish lip, yellow color Band 1 and Band 2s and 3 usually merged.

Two subspecific entities have been proposed, however, we recognized them as a single biological species, *A. xiengensis*.

1. Typical form: Band 1 reddish to brownish; Bands 2 and 3 concurrent slanted brownish blotches continuous to expanded lip; Bands 4 and 5 brownish spiral band; Band 6 absent (Fig. 4.11A–C).
2. var. "*multifasciata*" Fulton, 1896: similar to the typical form, but Band 1 yellowish; Bands 2 and 3 usually divided into several smaller bands; Band 6 reddish (Fig. 4. 11G, H, and Sutcharit et al., 2015: fig. 11f, g).
3. var. "*clausus*" Pilsbry, 1900: similar to the typical and var. "*multifasciata*", but Bands 2 and 3 disappeared and turned to pinkish stain on second half of last whorl (Fig. 4.11D–F).

***Amphidromus* (*Syndromus*) *fuscolabris* Möllendorff, 1898**

Figs 4.1, 4.9E, F, 4.11J–M, 4.13C, D, 4.14G–I, Table 4.1

Amphidromus zebrinus fuscolabris Möllendorff, 1898: 75. Type locality: Boloven [Boloven Plateau, Paksong District, Champasak, Laos]. Pilsbry 1900: 199, 200. Zilch 1953: 134, pl. 23, fig. 22. Laidlaw and Solem 1961: 564, 621. Richardson, 1985: 49.

Material examined

Holotype SMF 7641 (Fig. 4.11I). Ban Phone, La-Marm District, Sekong, Laos: CUMZ 7040 (34 shells, typical form; Fig. 4.11J, K), 7041 (2 specimens in ethanol; Figs 4.9E, 4.13D, C, 4.14G–I), 7042 (73 adult shells + 10 juvenile shells, yellowish form; Fig.

4.11L, M), 7043 (2 specimens in ethanol; Fig. 4.9F). Ban Xai Na Pho, Phatumphone, Champasak, Laos: CUMZ 7044 (2 shells).

Description

Shell sinistral, elongated conic, rather solid and glossy. Spire elongated conic; apex cute, tint-pink to brownish without black spot on the tip. Whorls 6 to 7, nearly smooth; suture wide and shallow; last whorl rounded. Periostracum transparent to thin corneous with greenish streaks on lower half of last whorl. Last whorl shows yellow to orange Band 1; Bands 2 to 5 merged and become black or brown six to seven slanted blotches; Band 6 yellow; varix absent. Parietal callus thickened with bright purplish-pink. Aperture elongated auriform; peristome thickened, expanded and not reflected; lip purplish-pink. Columella rather thick, straight, dilated and purplish-pink. Umbilicus imperforated.

Radula

Each row contains about 161 (80-(35-31)-1-(31-35)-80) teeth. Central tooth unicuspid with curved cusp. Lateral and marginal teeth almost similar to that described in *A. areolatus*. Marginal teeth start from lateral tooth 17 to 21 outwards (Fig. 4.14G–I).

Genital organs

Atrium (at) slightly long (n = 10). Penis (p) long cylindrical and and slightly swollen at distal end. Epiphallus (e) short, half of penis length; flagellum (fl) about same length with epiphallus and terminated with pointed tip. Appendix absent. Penial retractor muscle (pr) thin and long. Vas deferens (vd) very narrow tube connected between epiphallus and free oviduct (Fig. 4.13C).

Internal penial wall corrugated into strong penial pilasters, which form fringe around penial verge. Penial verge conic, smooth surface and orifice open near the tip (Fig. 4.13D).

Vagina cylindrical, long slender, about two times longer than penis. Gametolytic duct long, proximal to genital orifice of a relatively larger diameter than vagina and

distally tapering; distal to genital orifice small tube of about same length of proximal part and connected to gametolytic sac. Oviduct and albumin gland very small (Fig. 4.13C).

Internally, vaginal wall shows longitudinal vaginal pilasters (vp); proximal to genital orifice, with thin wall and smooth surface, and distally pilasters show continuous ridges (Fig. 4.13D).

Distribution

The original description of the species was described by Möllendorff (1898), the type locality was from Boloven, Laos. Unfortunately, we did not get any specimen from the type locality in a recent survey. The specimens were collected from a mountain at Ban Phone (Phone village), Sekong Province, and Ban Xai Na Pho (Xai Na Pho village) Phatumphone, Champasak, Laos, which are both located at a lower altitude than Boloven Plateau. It seems that this species is only found in low altitude habitats.

Remarks

Amphidromus fuscolabris differs from *A. zebrinus* and *A. eudeli* by having a large and elongate shell, apex tint-pink, purplish-pink parietal callus, Band 1 yellowish, Bands 2 to 5 merged and become 6 to 7 slanted blotches (on last whorl). In comparison, *A. zebrinus* (see Sutcharit et al., 2015: fig. 15k) has a smaller shell, Band 1 absent, Bands 2 and 5 merged and become fifteen narrow slanted stripes on last whorl, and reddish band in-between Bands 5 and 6. Whereas, *A. eudeli* (Fig. 4.11N, holotype RBINS 617427) has a smaller shell, thin parietal callus, Bands 2 and 3 merged and Bands 4 and 5 well present.

Two color forms were observed from Sekong, Laos. These are the typical form (Fig. 4. 11I-K) and the yellowish form that is monochrome yellowish with Bands 2 to 5 absent and stained with pale yellowish color, and Band 6 sometimes present as a brownish color (Fig. 4.11L, M). However, these two color forms show pinkish to purplish-pink parietal callus and columella, and have identical genital structures and

sculptures inside the penis and vagina. In addition, they occur sympatrically and so we recognized them as conspecific.

Amphidromus (*Syndromus*) *haematostoma* Möllendorff, 1898

Figs 4.1, 4.11O–R

Amphidromus haematostoma Möllendorff, 1898: 74, 75. Type locality: Boloven [Boloven Plateau, Champasak, Laos]. Pilsbry 1900: 182, 183. Zilch 1953: 132. Laidlaw and Solem 1961: 527, 625. Richardson 1985: 19.

Amphidromus haematostoma var. *viridis* Möllendorff, 1898: 75. Type locality: Boloven [Boloven Plateau, Champasak, Laos]. Pilsbry 1900: 183. Zilch 1953: 132, pl. 22, fig. 4. Laidlaw and Solem 1961: 527, 670. Richardson 1985: 19.

Amphidromus haematostoma var. *varians* Möllendorff, 1898: 75. Type locality: Boloven [Boloven Plateau, Champasak, Laos]. Pilsbry 1900: 183. Zilch 1953: 132, pl. 22, fig. 5. Laidlaw and Solem 1961: 527, 668. Richardson 1985: 19.

Amphidromus (Syndromus) haematostomus—Lehmann and Maassen 2004: 20.

Type materials

The species description included two varieties, "var. A. *viridis*" and "var. B. *varians*", but only one set of shell measurements was given in the original description of the nominotypical variety. The specimen SMF 7559 labelled as "var. A. *viridis*" exactly matches the dimensions given in the original description. Therefore, we believe this implied that "var. A. *viridis*" specimens are the type series of *A. haematostomus* s.s. The specimen SMF 7559 (Fig. 4.11O) was designated as the lectotype in Zilch (1953: 132, pl. 22, fig. 4), which is considered to be a valid lectotype designation of the species, and the other specimen from the same lot becomes the paralectotype SMF 5760 (1 shell; Fig. 4.11P).

The other specimens labelled as "var. B. *varians*" are distinct variants and are, therefore, excluded from the type series of this nominal species (ICZN 1999: Art. 72.4.1. The specimen SMF 7561 (Fig. 11Q) was designated as the lectotype in Zilch (1953: 132, pl. 22, fig. 5), which is considered to be a valid lectotype designation of "var. B. *varians*"

and another specimen from the same lot became the paralectotype SMF 5762 (1 shell; Fig. 4.11R).

Other material examined

Boloven Plateau, Pakxong District, Champasak, Laos: RMNH 101050 (6 adults + 2 juveniles), two lots in W.J.M. Maassen collection (8S) and (12 adults + 2 juveniles). Boloven, Annam: NHMUK 1899.4.22.74 (1 shell). On coffee plantation, near Pakxong, Boloven Plateau, Champasak, Laos: ZMB ex. Lehmann collection (15 shells), ZMB ex. Lehmann collection (5 adults + 1 juvenile).

Remarks

This species is currently known only from the type locality. The shell characters are clearly distinct from all other recognized species. Shell sinistral and ovated conic. Apex acute with black spot on the tip. Last whorl rounded; shell color with monochrome greenish (faded in old specimen), and yellowish subsutural band and umbilical area. Aperture ovate; peristome expanded and little reflected; lip reddish-purple. Parietal callus reddish-purple and thickened; columella reddish-purple and dilated; umbilicus imperforated.

Laidlaw and Solem (1961) suggested that this species was probably a junior synonym of *A. roseolabiatus*. However, after comparing with type specimens of both species and among recently collected specimens of *A. roseolabiatus*, *A. haematostoma* clearly differs from *A. roseolabiatus* in having ovated conic shape, uniform greenish to yellowish shell, yellowish subsutural and umbilical area, thickened parietal callus, lip widely expanded, and reddish-purple lip and parietal callus. While, *A. roseolabiatus* exhibits an elongated conic shell, greenish radial streaks, white subsutural band, transparent parietal callus, and lip pinkish or white and expanded.

Lehmann and Maassen (2004: 20) recorded the genital characters (without illustration) of the topotypic population and mentioned that “very short flagellum and a short conical verge”. These are the distinguished characters of this subgenus. However, further investigation of the genitalia is necessary to confirm the subgeneric status.

***Amphidromus* (*Syndromus*) *xiengkhaungensis* Inkhavilay & Panha sp. nov.**

Figs 4.1, 4.11S, T, Table 4.1

Etymology. The specific name "*xiengkhaungensis*" is derived from the type locality of this new species.

Type material examined

Holotype CUMZ 7045 (Fig. 4.11S). Measurement: shell height 25.61 mm, shell width 15.58 mm, and with 6 whorls

Paratypes CUMZ 7046 (10 shells, Fig. 4.11T), NHMUK (2 shells).

Type locality. Limestone outcrop at Ban Nong Tang, Phou Kood District, Xieng Khaung, Laos (19° 30' 59.2" N, 102° 53' 37.6" E), and 1140 m amsl.

Diagnosis

The new species is superficially similar to *A. roemeri*, but the distinguishing characters are a relatively large and thick shell, dark to brownish spire, Bands 2 and 3 merged and become tint-pink stained, with a pale tint-pink lip. Whereas, *A. roemeri* shows a relatively small and thin shell, whitish ground color, Bands 2 and 3 absent, and has a white lip. *Amphidromus xiengkhaungensis* sp. nov. differs from *A. sinensis* and *A. flavus* by having an ovated conic shell, Bands 2 and 3 stained with tint-pink, ovated aperture and slightly angular last whorl. In comparison, *A. sinensis* and *A. flavus* have an elongated conic, relatively small and thin shell, yellowish color, and rounded last whorl. In addition, *A. globonevilli* differs from this new species by having a small and thin shell, yellowish color, last whorl rounded and Bands 2 and 3 absent.

Description

Shell sinistral, ovated conic, rather thick and glossy. Apex acute, tint-pink color; spire conic with dark color; suture wide and depressed. Whorls 5 to 6 nearly smooth; last whorl slightly angular. Periostracum thin corneous and transparent. Earlier whorls with darker color; varix absent. Shell banding without Band 1; Bands 2 and 3 merged

and become tint-pink stained; Bands 4 and 5 dark brown; Band 6 absent. Parietal callus thin and transparent to slightly thick and white. Aperture ovated; peristome expanded and little thickened; lip pale tint-pink to white. Columella straight, thickend and white. Umbilicus rimed.

Remarks

Amphidromus xiengkhaungensis sp. nov. is currently known only from the type locality, a dry green forest and isolated limestone forest surrounded by a reservoir and agricultural areas. The empty shells were found on the floor among the leaf litter. Unfortunately, no living specimens have been collected.

Discussion

The first *Amphidromus* species from Laos, *A. roemeri*, was described in Laos by Pfeiffer in 1863. Subsequently, *A. xiengensis*, *A. laosianus* and *A. haematostoma* were reported by Morlet (1891), Bavay (1898) and Möllendorff (1898), and the latest described species was *A. protania* by Lehmann and Maassen (2004) that was collected from Ban Donxé, Salavan Province. However, there are many species for which basic information is still unclear, such as the type locality. For example, for *A. roemeri* the author stated only "Laos Mountain" as the locality. Almost all records were from southern areas or lowlands, except for *A. xiengensis* that was recorded in the north (Fig. 4.1).

In this paper we described two new species that both are known only from the type localities. *Amphidromus syndromoideus* sp. nov. having a small shell size, dextral and sinistral, green color with long epiphallus and flagellum, and very long appendix. *Amphidromus xienkhaungensis* sp. nov. is described using only shells. The shell is superficially similar to *A. roemeri* but it is larger and thicker with a dark to brown spire. Moreover, the two recorded species *Amphidromus xiengensis* and *A. flavus* were described using shells and genital anatomy.

In the southern part of Laos we collected the four species *A. givenchyi*, *A. fuscolabris*, *A. areolatus* and *A. xiengensis*. The most dominant species were *A. givenchyi*, *A. fuscolabris* and *A. areolatus*, which could be found in between altitude

140–190 m amsl. Only two species were collected in the central region of Laos, *A. roseolabiatus* and *A. syndromoideus* sp. nov., with the most dominant species being *A. roseolabiatus*, while *A. syndromoideus* sp. nov. is known only in the type locality. In the northern part of Laos we collected five species of *Amphidromus;* surprisingly *A. roseolabiatus* and *A. xiengensis* were found in both southern and northern Laos, but *A. flavus*, *A. pervariabilis*, and *A. xiengkhuangensis* sp. nov. were only found in northern Laos from Vang Viang to Phongsaly.

Amphidromus roseolabiatus and *A. xiengensis* were the most dominant and widely distributed species throughout Laos. They can be found in several habitats, even in limestone areas from the south to the north. However, *A. givenchyi*, *A. syndromoideus* n. sp and *A. xiengkhaungensis* sp. nov. were specific to their unique habitats, where *A. givenchyi* was restricted to the Salavan Province (southern Laos), *A. syndromoideus* sp. nov. is only found at the type locality Khammouan Province (central Laos) and *A. xiengkhaungensis* sp. nov. is rare and only found in an isolated limestone area at Nong Tang Village, Xieng Khaung Province, which is in between the northern and central border at 800 m amsl.

The occurrence of *A. roseolabiatus* and *A. xiengensis* in the southern, central and northern parts of Laos may suggest (i) they originally have a widespread origin, (ii) one or both have been translocated by humans or (iii) they have been subjected to long range dispersal. These hypotheses await to be resolved.

The results show that the *Amphidromus* species diversity in Laos is low compared to in Thailand (Panha 1996; Sutcharit et al., 2015) and Vietnam (Schileyko 2011) at 19 and 23 species, respectivt al.

ely. However, this may simply reflect the deficient surveying time and sampled sites in Laos compared to the other two countries rather than the actual species diversity. Thus, more extensive (intensity and coverage) sampling is required.

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Figure 4.1 Distribution map of *Amphidromus* spp. in Laos recognized by this study.

Figure 4.2 Living snails. **A, B.** *Amphidromus roseolabitus*. (**A**) CUMZ 7012 the typical form from Ban Phavong, Khammouan, Laos and (**B**) CUMZ 7005 Tam Mung Korn, Bolikhamxay, Laos. **C.** *Amphidromus givenchyi* CUMZ 7018 from Thad Lor Waterfall, Salavan, Laos. **D**. *Amphidromus syndromoideus* n. sp. holotype CUMZ 7019, from type locality.

Figure 4.3 Aestivation sites of *Amphidromus* species. **A, B.** *Amphidromus roseolabiatus* (shell height about 34 mm) from NamTurn Bridge, Bolikhamxay, Laos aestivated. (**A**) inside the sterile frond of stag horn ferns *Platycerium* and (**B**) in a small hole on the Jackfruit tree trunk *Artocarpus heterophyllus* Lam., with other snails *Quantula* and *Durgella*. **C.** *Amphidromus givenchyi* (shell height about 43 mm) hiding in a small hole of dipterocarpus tree shell. **D.** *Amphidromus syndromoideus* n. sp. (shell height about 28 mm) from the type locality hiding in a hole of tree after removal the clusters of sterile frond of basket ferns *Drynaria*.

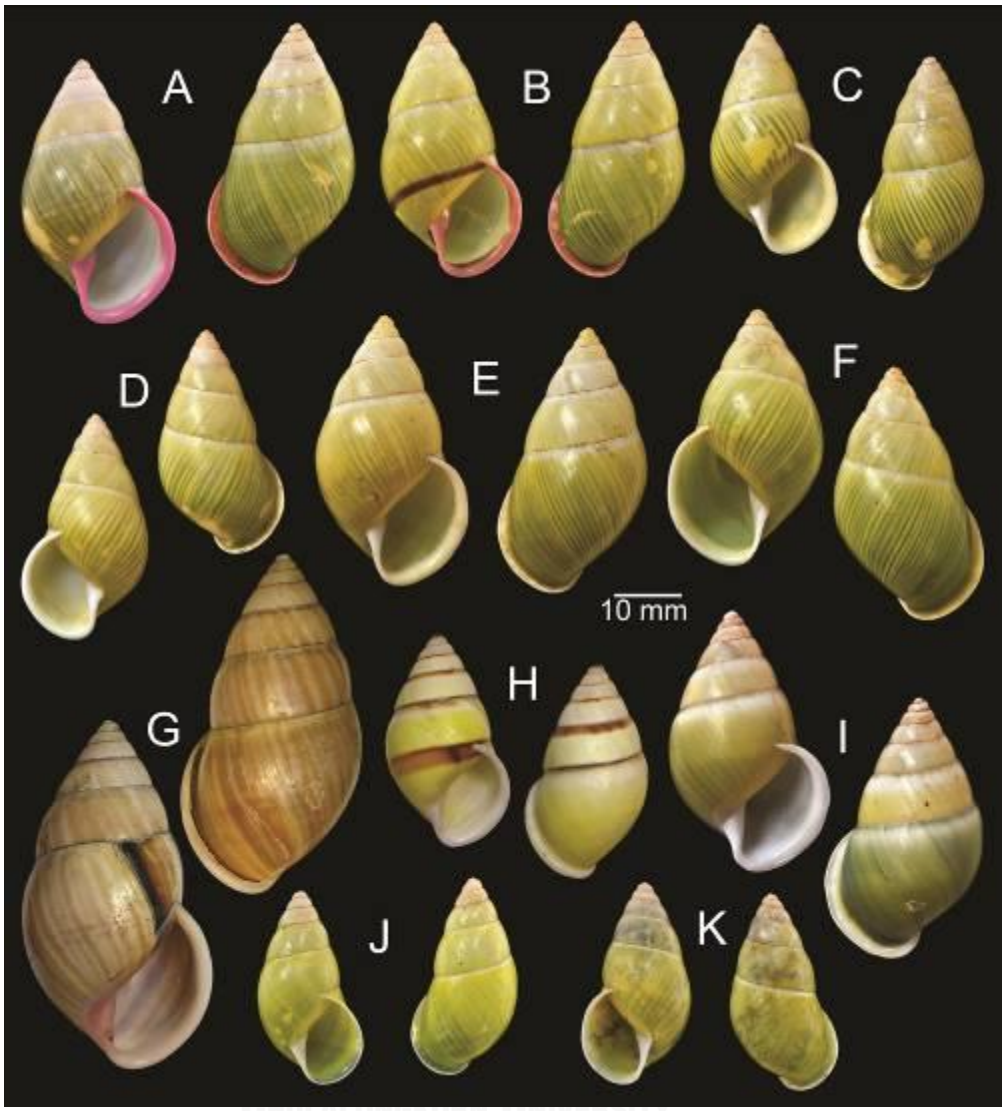

Figure 4.4 Shells of *Amphidromus* (*Amphidromus*) spp. **A–F.** *Amphidromus roseolabiatus*. (**A, B**) CUMZ 7011 the typical form from Ban Phavong, Khammouan, Laos and (**C, D**) CUMZ 7006 from Nam Turn Bridge, Bolikhamxay, Laos and (**E, F**) CUMZ 7004 white lip form from Tam Mung Korn, Bolikhamxay, Laos. **G.** *Amphidromus laosianus*, RMNH 101049 from Khone, Champasak, Laos. **H.** *Amphidromus protania*, holotype RMNH 98143. **I.** *Amphidromus givenchyi*, CUMZ 7015 from Thad Lor Waterfall, Salavan, Laos. **J, K.** *Amphidromus syndromoideus* n. sp. (**J**) holotype CUMZ 7019 and (**K**) paratype CUMZ 7020 from type locality.

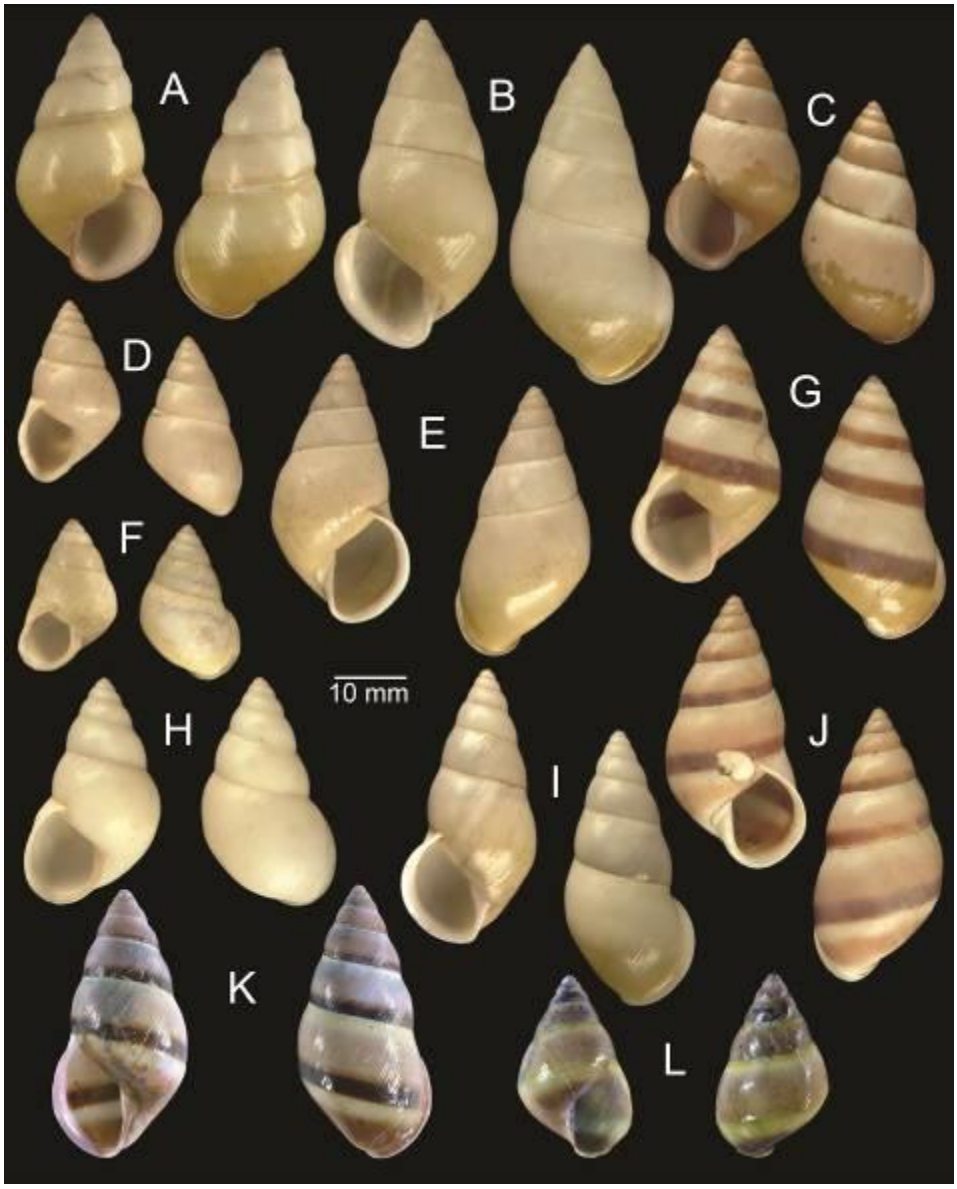

Figure 4.5 Shells of *Amphidromus pervariabilis*. **A, B.** Syntype of the nominotypical form MNHM-IM-2000-2049. **C.** var. "*bifasciata*", syntype MNHM-IM-2000-2059. **D.** var. "*goniostoma*", syntype MNHM-IM-2000-2058. **E.** var. "*lilacina*", syntype MNHM-IM-2000-2052. **F.** var. "*minor*", syntype MNHM-IM-2000-2050. **G.** var. "*monozonalis*", syntype MNHM-IM-2000-2057. **H.** var. "*obesa*", syntype MNHM-IM-2000-2053. **I.** var. "*protracta*", syntype MNHM-IM-2000-2051. **J.** var. "*tricolor*", syntype MNHM-IM-2000-2054. **K, L.** Specimens CUMZ 7014 from Khua District, Phongsaly, Laos.

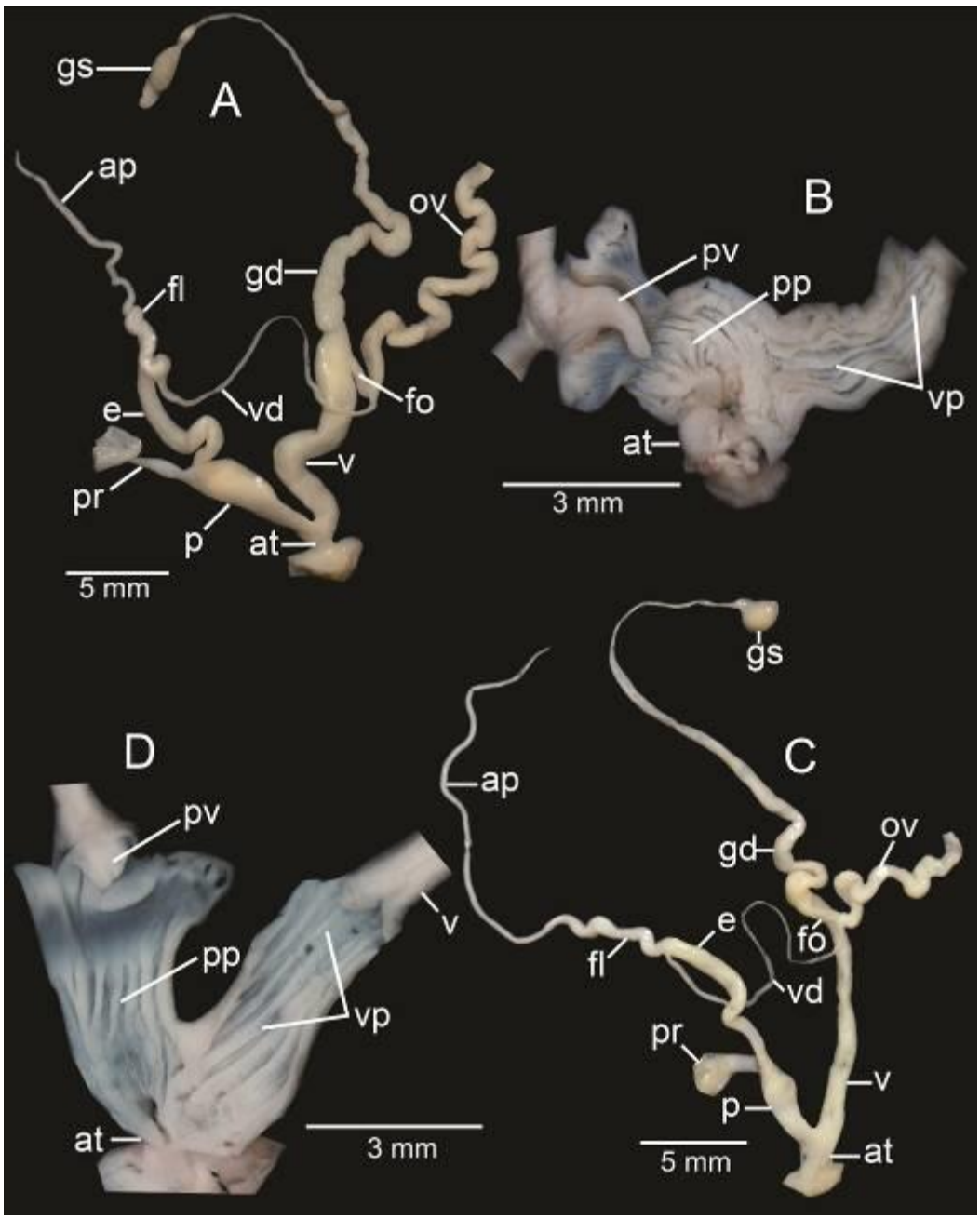

Figure 4.6 Genitalia of *Amphidromus* spp. **A, B.** *Amphidromus reoseolabiatus*, CUMZ 7012 from Ban Phavong, Khammouan, Laos showing reproductive system and interior structures of penis and vaginal chamber. **D, C.** *Amphidromus syndromoideus* n. sp., holotype CUMZ 7019 showing the general characteristics of genital system and interior structures of penis and vagina chamber.

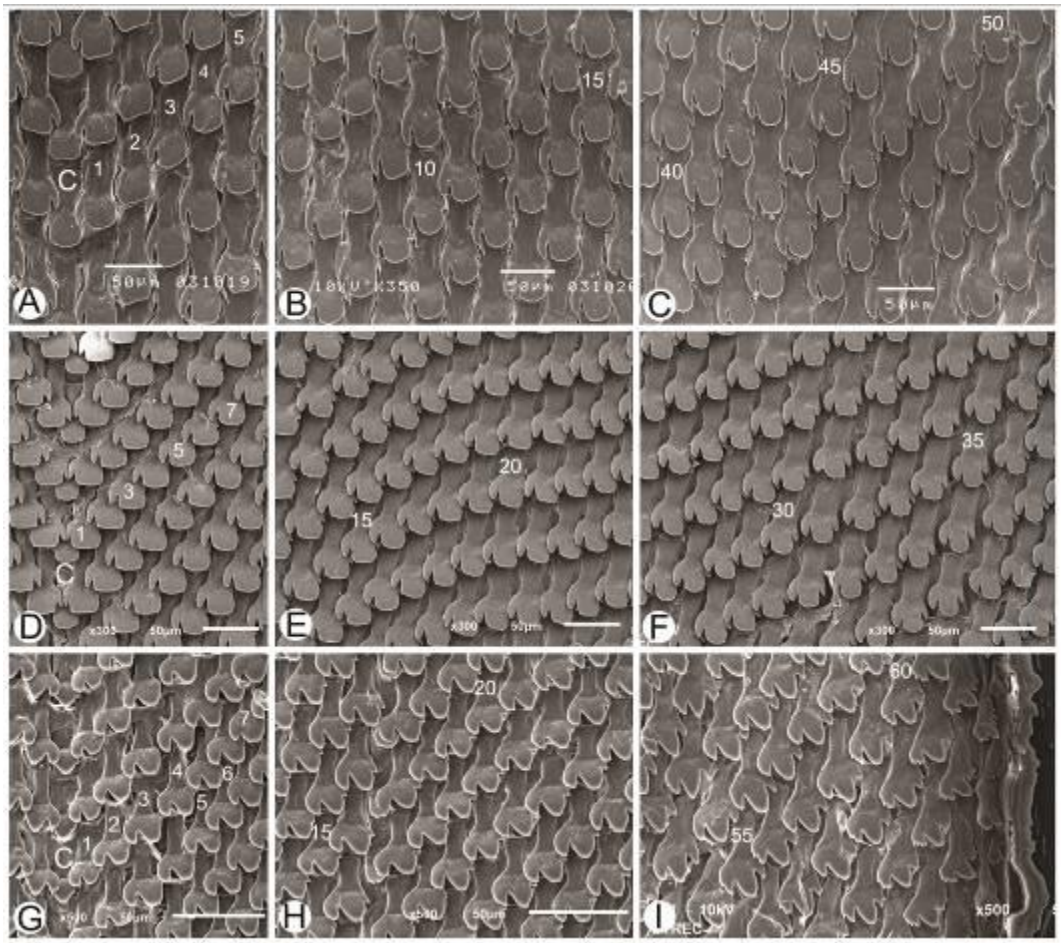

Figure 4.7 SEM images of the radula of **A–C.** *Amphidromus roseolabiatus*, CUMZ 7012 from Ban Phavong, Khammouan, Laos. **D–F.** *Amphidromus syndromoideus* n. sp., holotype CUMZ 7019. **G–I.** *Amphidromus areolatus*, CUMZ 7023 from Thad Fek, Attapue, Laos. (**A, D, G**) central tooth with the first to fifth to eighth lateral teeth, (**B, E, H**) lateral teeth with the tricuspid marginal teeth transition, and (**C, F, I**) outermost marginal teeth. Numbers indicated order of lateral and marginal end. Central tooth indicated by 'C'.

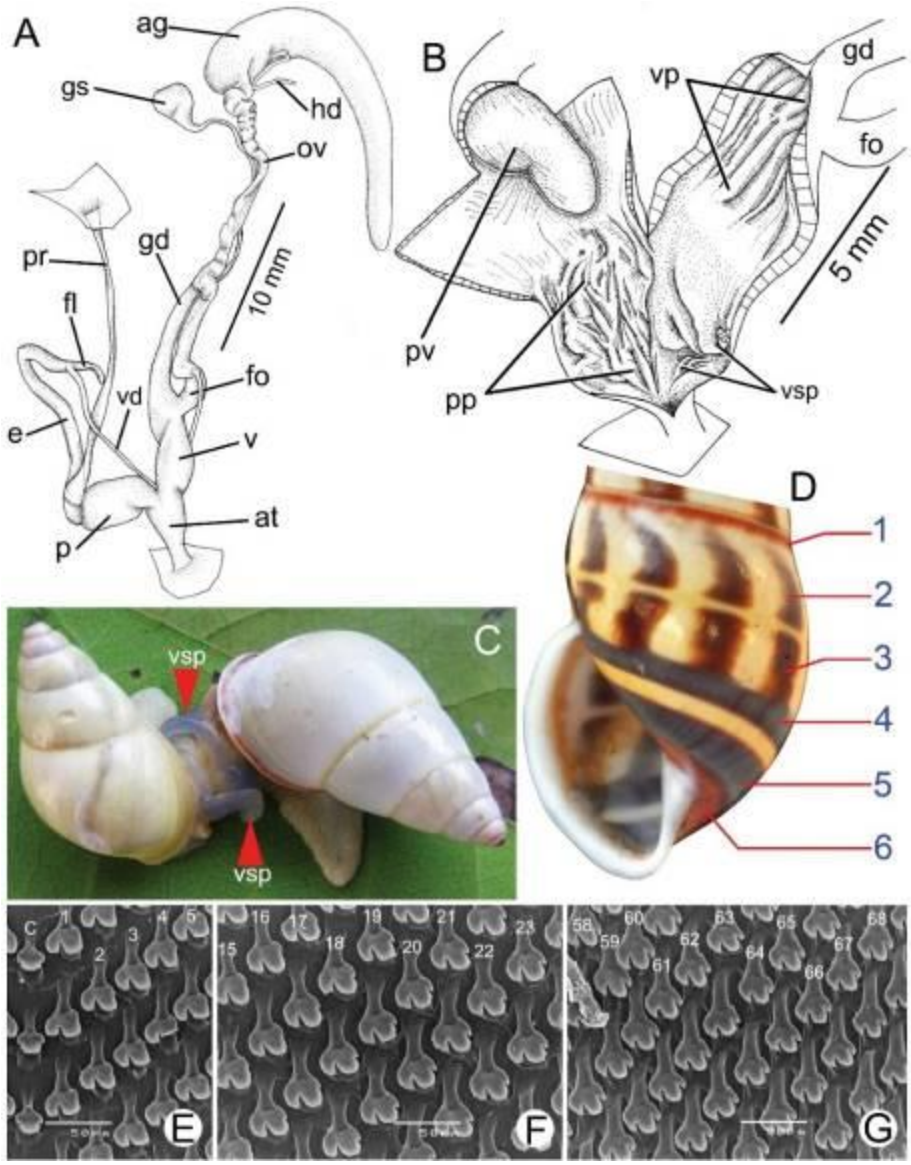

Figure 4.8 Genitalia, mating pairs, shell banding formula and radula morphology. **A, B.** *Amphidromus (Syndromus) contrarius*, ZMA collection from Timor, (**A**) genital system and (**B**) internal structures of penis and vagina. **C.** Mating pairs of *Amphidromus (Syndromus)* sp. shows the protruded vaginal simulator pilaster (vsp, red arrows) and it possible function as stimulating organ. **D.** Schematic of shell banding and the numbers 1 to 6 on last whorl indicate the position of each band. **E–G.** Radula morphology of *Amphidromus (Syndromus) contrarius* ZMA collection from Timor, (**E**) central tooth with the first to fifth lateral teeth, (**F**) lateral teeth with the tricuspid marginal teeth transition and (**G**) outermost marginal teeth. Numbers indicated order of lateral and marginal end. Central tooth indicated by 'C'.

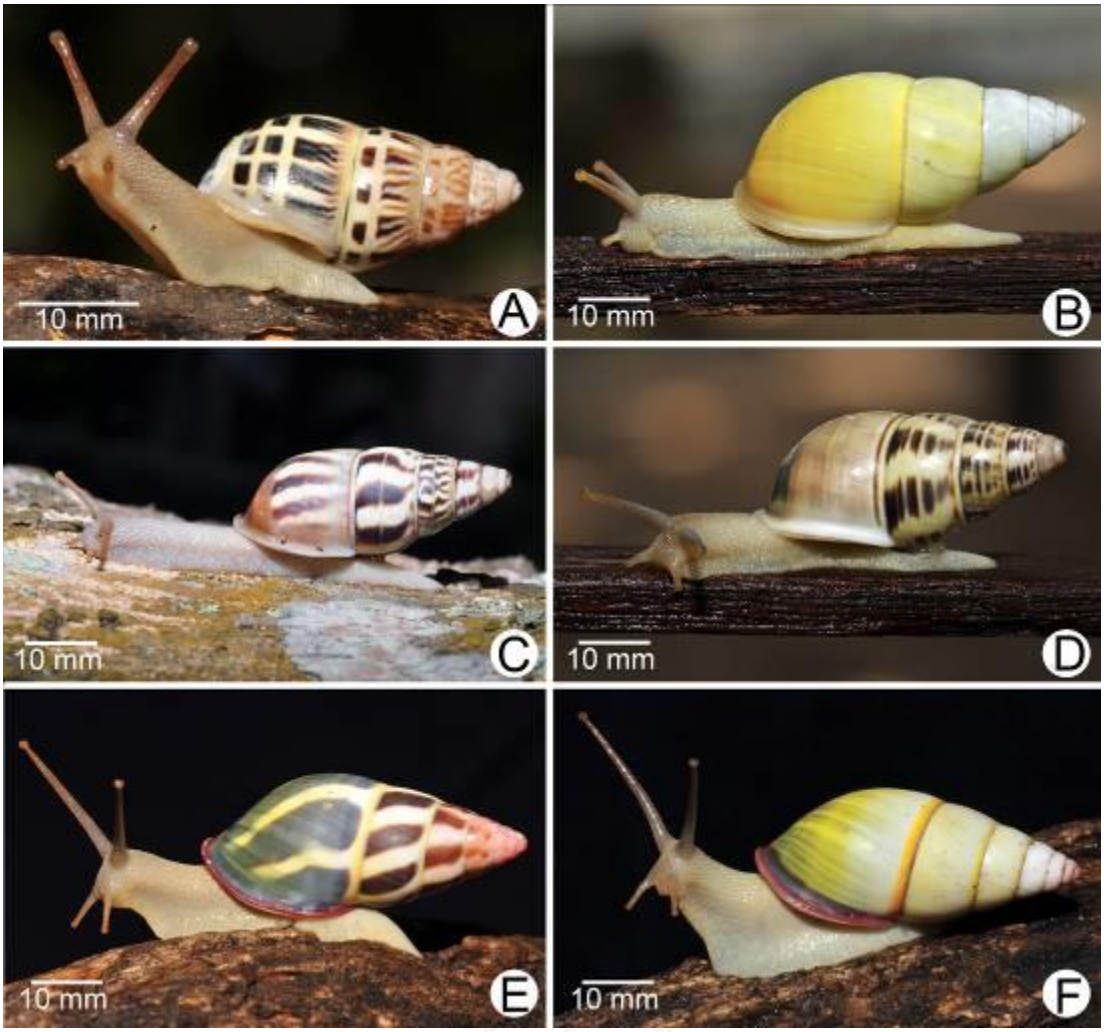

Figure 4.9 Living snails of *Amphidromus* (*Syndromus*) spp. **A.** *Amphidromus areolatus*, CUMZ 7023 from Thad Fek, Attapeu, Laos. **B.** *Amphidromus flavus*, CUMZ 7027, from Ban Na Deauy, Luang Phrabang, Laos. **C, D.** *Amphidromus xiengensis* from Thad Kacham, Luang Phrabang, Laos CUMZ 7035, the typical form, and var. "*multifasciata*" respectively. **E, F.** *Amphidromus fuscolabris*, CUMZ 7041, 7042 from Ban Phone, Sekong, Laos, (**E**) the typical colour form and (**F**) monochrome yellowish colour form.

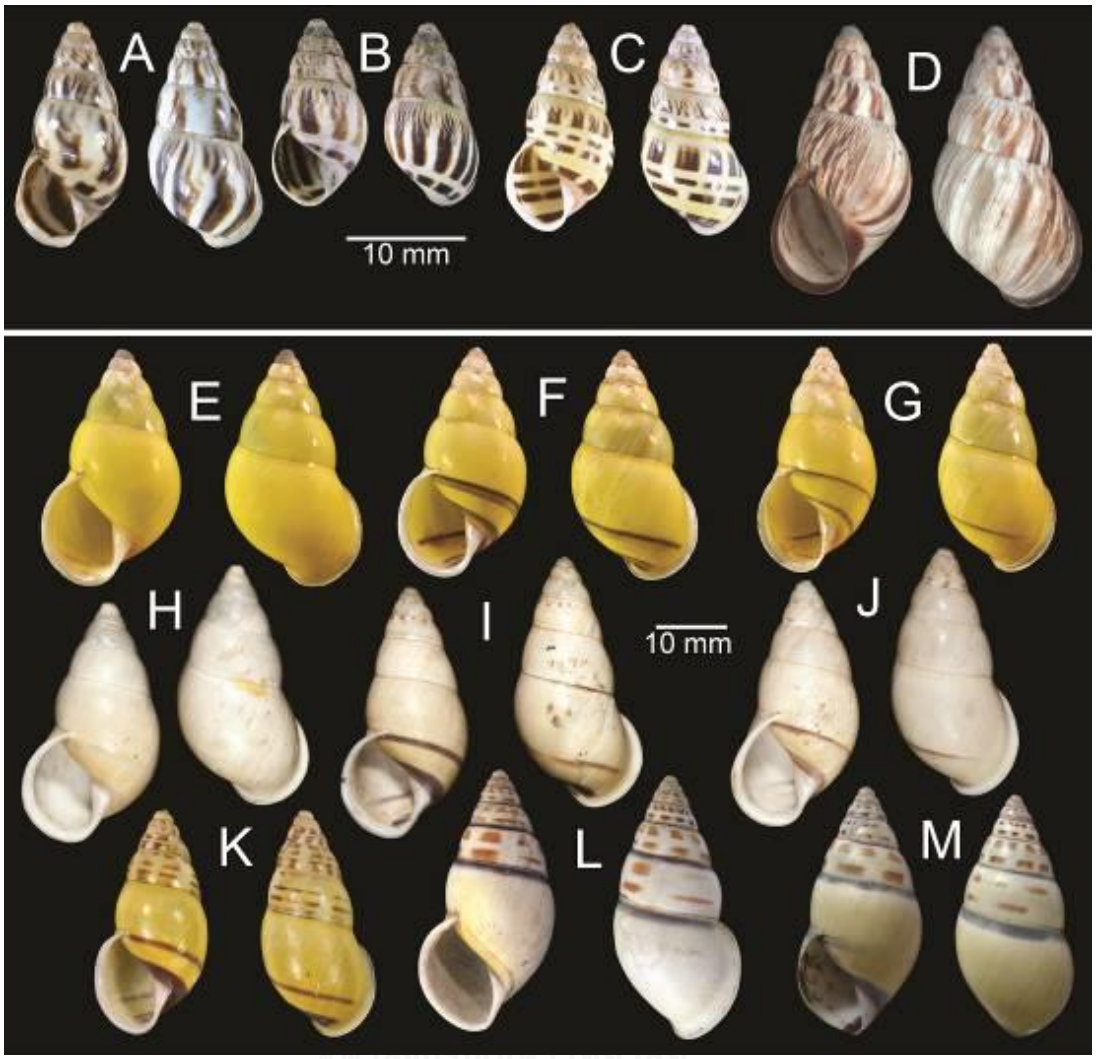

Figure 4.10 Shells of *Amphidromus* (*Syndromus*) spp. **A–C.** *Amphidromus areolatus*, CUMZ 7022 from Thad Fek, Attapeu, Laos. **D.** *Amphidromus begini* (Morlet, 1886), syntype MNHN-IM-2000-1832 from Strung-Trang, Cambodia. **E-G.** *Amphidromus flavus*, CUMZ 7029 from Tam Pou Kham, Vientiane, Laos. **H.** *Amphidromus flavus* var. "*indistinctus*", holotype ANSP 31486. **I-K.** *Amphidromus flavus* var. "*tryoni*", (**I**) lectotype ANSP 31488, (**J**) paralectotype ANSP 252745 and (**K**) specimen CUMZ 7026 from Ban Na Deauy, Luang Phrabang, Laos. **L, M.** *Amphidromus semitessellatus*, lectotype MNHN-IM-2000-1985 and (**M**) specimen NHMUK collection from Cambodia.

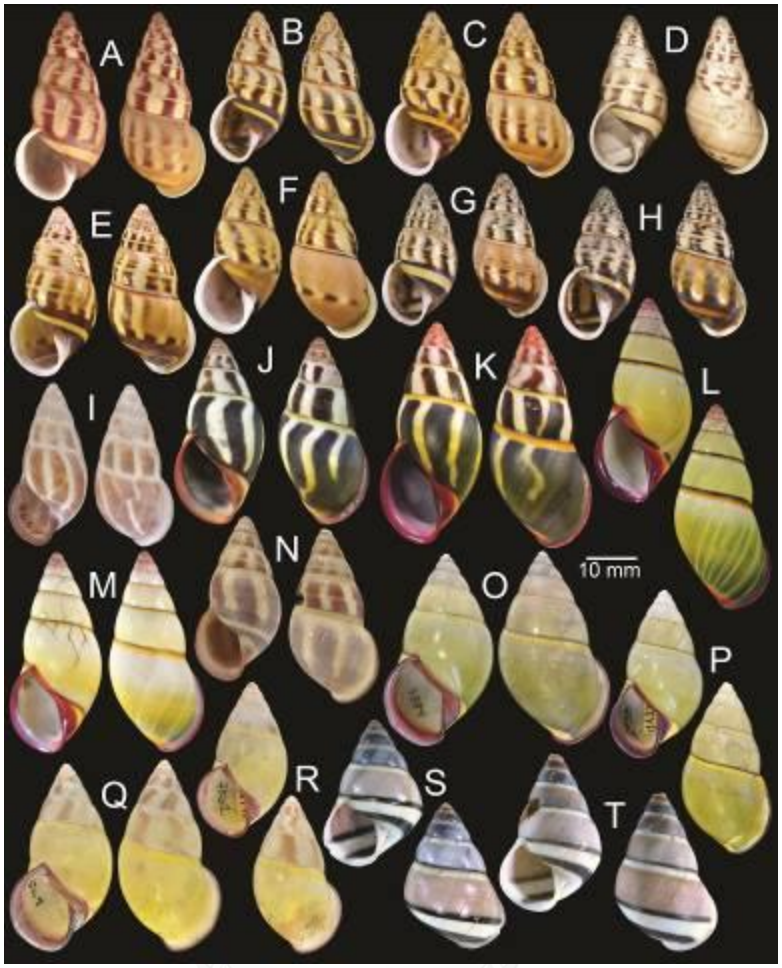

Figure 4.11 Shells of *Amphidromus* (*Syndromus*) spp. **A–C.** *Amphidromus xiengensis*, (**A**) Lectotype MNHNIM-2000-5249, (**B**) CUMZ 7050 from Thailand and (**C**) CUMZ 7034 from Tam Chiang Dao, Chiangmai, Thailand. **D-F.** *Amphidromus xiengensis* var.“*clausus*”, (**D**) lectotype ANSP 31496, (**E**) CUMZ 7036 from Ban Na Deauy, Luang Phrabang, Laos and (**F**) CUMZ 7052 from Pha Tang, Chiangrai, Thailand. **G, H.** *Amphidromus xiengensis* var. “*multifasciata*”, CUMZ 7038 from Phu Nang National Park, Phayao, Thailand. **I–M.** *Amphidromus fuscolabris*, (**I**) holotype SMF 7641 and (**J–M**) specimens CUMZ 7041, 7042 from Ban Phon, Sekong, Laos. **N**. *Amphidromus eudeli*, syntype RBINS 617427 from Binh Dinh, Annam. **O, P.** *Amphidromus haematostoma*, (**O**) lectotype SMF 7559 and (**P**) paralectotype SMF 7560. **Q, R.** *Amphidromus haematostoma* var. “*varian*”, (**Q**) lectotype SMF 7561 and (**R**) paralectotype SMF 7562. **S, T.** *Amphidromus xiengkhaungensis* n. sp. (**S**) holotype CUMZ 7045 and (**T**) paratype CUMZ 7046.

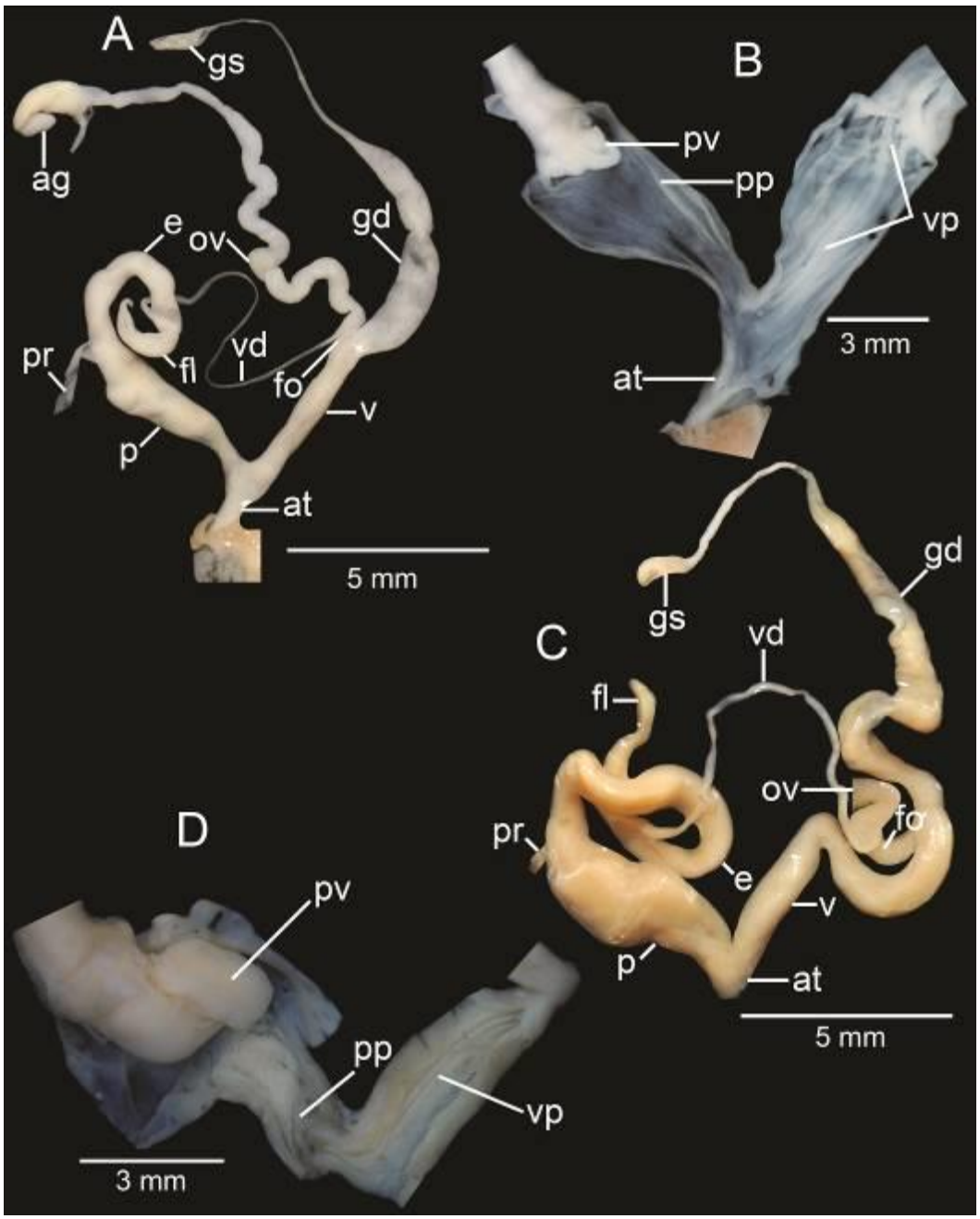

Figure 4.12 Genitalia of *Amphidromus* (*Syndromus*) spp. **A, B.** *Amphidromus areolatus*, CUMZ 7023 from Thad Fek, Attapeu, Laos showing the reproductive system and interior structures of the penis and vaginal chamber. **D, C**. *Amphidromus flavus*, CUMZ 7027 from Ban Na Deauy, Luang Phrabang, Laos showing the general characteristics of the genital system and the interior structures of the penis, atrium and vagina chamber.

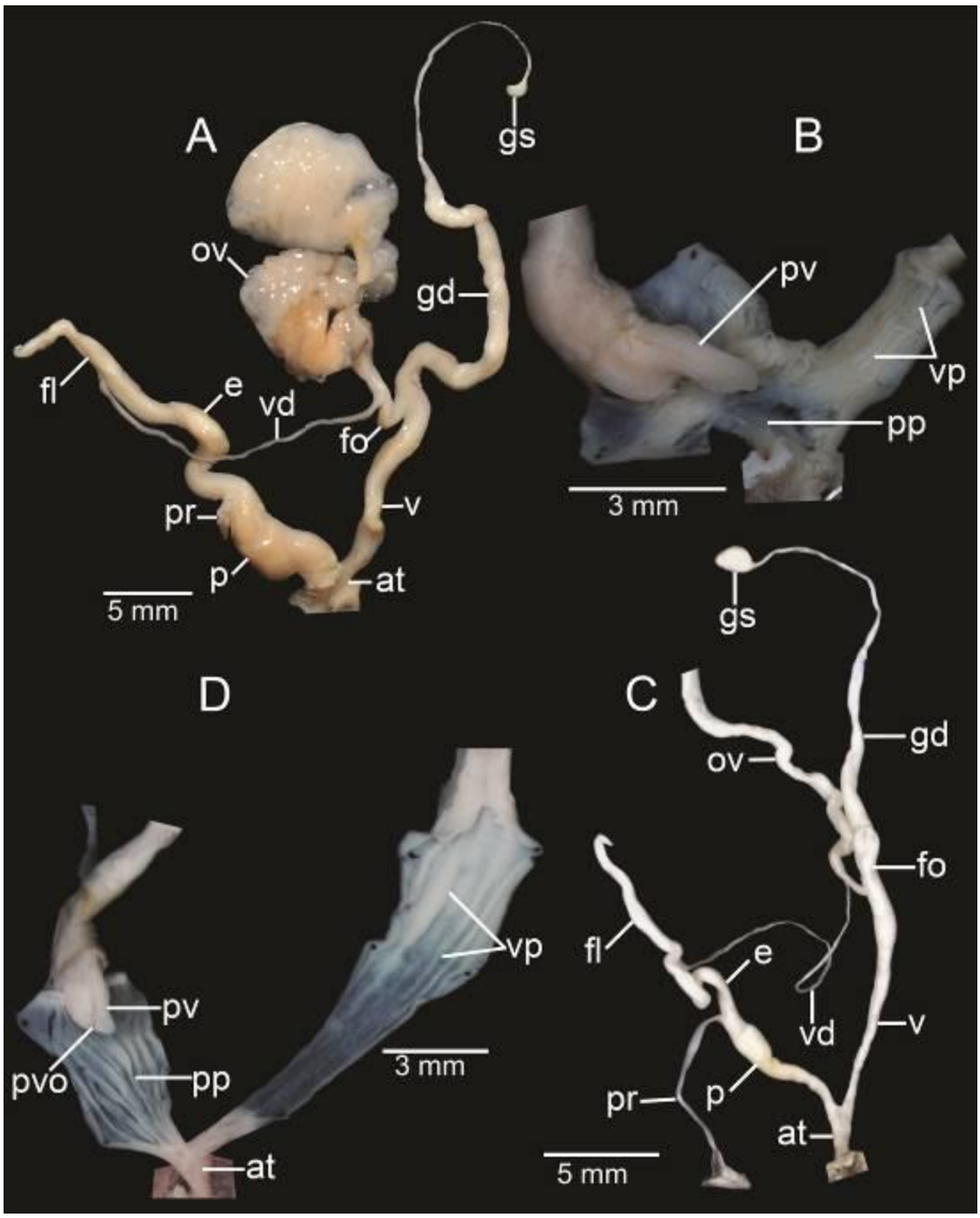

Figure 4.13 Genitalia of *Amphidromus* (*Syndromus*) spp. **A, B.** *Amphidromus xiengensis*, CUMZ 7035 from Luang Phrabang showing the reproductive system and interior structures of the penis and vaginal chamber. **D, C**. *Amphidromus fuscolabris*, CUMZ 7041 from Ban Phone, Sekong, Laos showing the general characteristics of the genital system and the interior structures of the penis, atrium and vagina chamber.

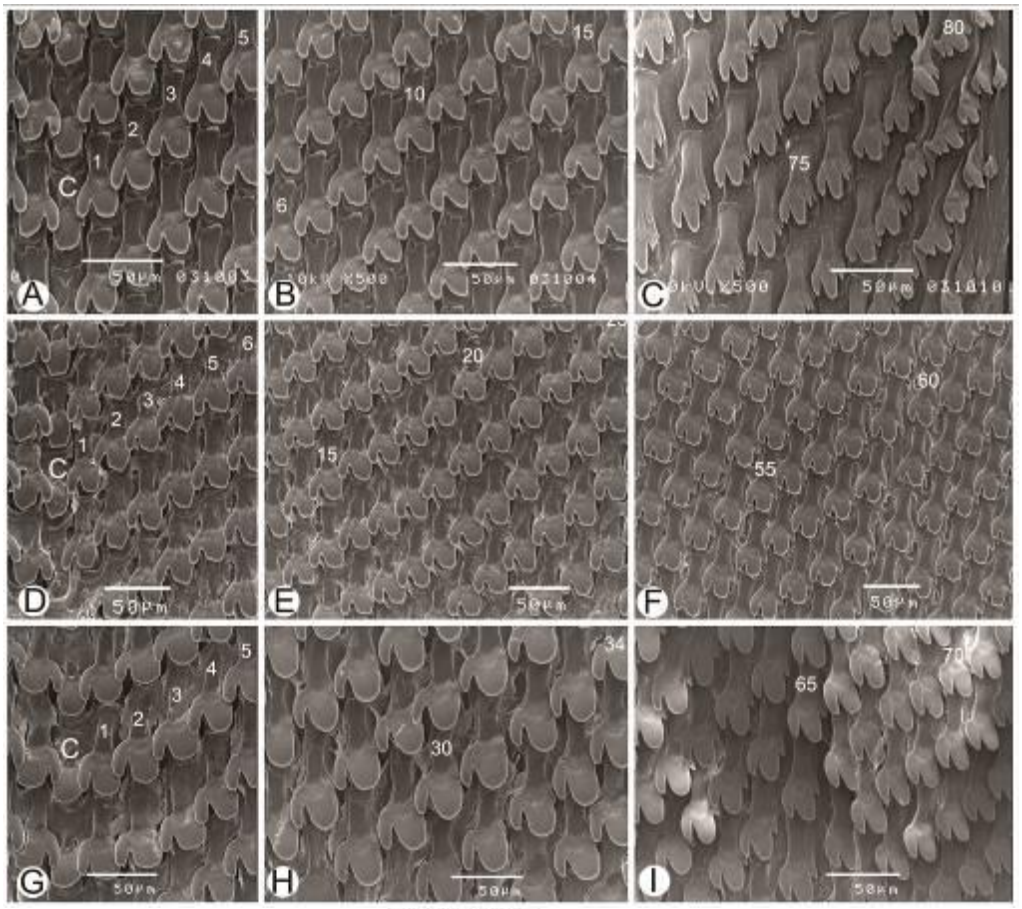

Figure 4.14 SEM images of the radula of **A–C.** *Amphidromus flavus*, CUMZ 7027 from Ban Na Deauy, Luang Phrabang, Laos. **D–F.** *Amphidromus xiengensis*, CUMZ 7037 from Ban Na Deauy, Luang Phrabang, Laos. **G–I.** *Amphidromus fuscolabris*, CUMZ 7041 from Ban Phone, Sekong, Laos. (**A, D, G**) central tooth with the first to fifth or sixth lateral teeth, (**B, E, H**) lateral teeth with the tricuspid marginal teeth transition, and (**C, F, I**) outermost marginal teeth. Numbers indicated order of lateral and marginal end. Central tooth indicated by 'C'.

Table 4.1 Shell measurements of ten *Amphidromus* species from Laos. Specimen collections and catalogue numbers are indicated in parentheses.

Species, locality and CUMZ nos.	No. of specimens	Range, mean ± S.D. in mm of:			Number of whorls
		Shell height	Shell width	H/W ration	
***Amphidromus roseolabiatus* Fulton, 1896**					
Ban Pha Vong, Khammouan: (7011, 7012)	21	28.0–41.6	14.6–21.2	1.8–2.2	6–6½
		35.7±3.24	17.9±1.74	1.9±0.09	
Km 70 Lao-Vietnam border, Khammouan: (7008)	4	28.0–35.3	15.5–19.0	1.4–2.2	6–6½
		33.4±3.57	17.1±1.48	1.9±0.34	
Tam Narng Lod, Khammouan: (7009)	5	33.6–40.1	16.7–19.1	1.9–2.2	6–6½
		36.8±3.17	17.9±1.03	2.0±0.10	
Tam Mung Korn, Khammouan: (7004, 7005)	22	28.2–40.0	14.1–21.7	1.7–2.0	6–6½
		37.2±2.40	20.2±1.52	1.8±0.10	
Thad Khaungsy, Luang phrabang: (7013, 7047, 7048)	6	34.3–41.8	17.8–19.8	1.9–2.1	6–6½
		37.5±2.71	18.8±0.87	1.9±0.07	
Nam Turn Bridge, Khmakert: (7006, 707)	9	26.1–34.2	15.2–17.5	1.6–2.0	6–6½
		30.3±2.31	16.3±0.75	1.8±0.14	
Ban Phone Can, Yommarat, Khammouan: (7001)	8	27.2–33.8	13.4–15.9	1.9–2.3	6–6½
		30.4±2.39	14.1±0.91	2.1±0.11	
Wat Paphar, Khamkert: (7002)	6	25.6–34.4	12.8–17.3	1.8–2.0	6–6½
		30.7±3.11	15.5±1.59	1.9±0.07	
Limestone Quarry, Bolikhamxay:(4013)	6	26.9–40.7	13.3–19.3	1.8–2.1	6–6½
		30.2±5.25	15.4±2.08	1.9±0.12	
Ban Phahom, Vang Vieng: (4017, 7049)	31	23.6–30.4	12.9–16.5	1.6–2.1	6–6½
		27.4±1.97	14.6±0.8	1.8±0.12	
***Amphidromus givenchyi* Geret, 1912**					
Thad Lor, Salavan: (7015, 7016)	110	23.3–43.6	11.8–22.9	1.7–2.1	7
		36.5±3.7	19.6±2.26	1.8±0.09	
Wat Phou, Salavan: (7017, 7018)	44	27.1–37.8	15.6–21.2	1.6–2.1	6–6½
		33.1±2.44	18.1±1.35	1.8±0.08	
***Amphidromus syndromoideus* sp. nov.**					
Tam Narng Ann, Khammouan: (7019, 7020, 7021)	20	21.8–29.1	11.2–14.2	1.7–2.2	6
		25.9±1.69	12.7±0.66	2.0±0.10	
***Amphidromus pervariabilis* Bavay and Dautzenberg, 1909**					
Ban Namly, Phongsaly: (7014)	3	31.5–40.9	18.6–19.6	1.6–2.2	7½
		37.2±5.02	19.0±0.54	1.9±0.31	

.....continued on the next page

Table 4.1 Shell measurements of ten *Amphidromus* species from Laos. Specimen collections and catalogue numbers are indicated in parentheses (Continued).

Species, locality and CUMZ nos.	No. of specimens	Range, mean ± S.D. in mm of: Shell height	Shell width	H/W ration	Number of whorls
***Amphidromus areolatus* (Pfeiffer, 1861)**					
Thad Fek, Attapeu: (7022, 7023)	33	13.3–21.8	7.1–10.2	1.5–2.2	6½
		16.9±2.19	8.5±0.74	1.9±0.13	
Thad Phasoam, Champasak (7024)	9	13.8–21.8	6.9–10.5	1.8–2.0	6½
		16.5±2.66	8.4±1.08	1.9±0.08	
***Amphidromus flavus* (Pfeiffer, 1861)**					
Wat Phousy, Luang Phrabang: (7025)	33	23.2–37.4	11.8–17.4	1.7–2.1	6½
		28.4±3.67	14.4±1.26	1.9±0.11	
Ban Na Deauy, Luang Phrabang:	11	22.2–29.8	12.1–14.2	1.8–2.3	6½
(7026, 7027)		25.7±2.27	12.9±0.68	1.9±0.17	
Mouhot's Tomb, Luang Phrabang: (7028)	5	24.4–29.0	13.1–13.9	1.7–2.2	6½
		27.6±1.88	13.5±0.36	2.0±0.17	
Tam Pou Kham, Vang Vieng: (7029)	12	23.7–35.5	13.0–17.1	1.7–2.2	6½
		28.3±3.48	14.3±1.35	1.9±0.14	
***Amphidromus xiengensis* Morlet, 1891**					
Ban Phon Pai, Champasak: (7030)	33	21.4–36.2	13.4–16.9	1.4–2.3	6½–7
		31.0±3.04	15.1±0.96	2.0±0.14	
Ban Oudom limestone, Oudomxay: (7032)	6	22.1–29.7	11.2–13.9	1.9–2.1	6½–7
		26.5±2.61	13.0±0.94	2.0±0.08	
Mouhot's tomb, Luang Phrabang: (7033)	5	21.9–35.2	12.0–14.8	1.8–2.3	6½–7
		28.1±5.03	13.2±1.43	2.1±0.21	
Thad Pha Soam, Boloven Plateau,	10	17.4–34.4	8.7–15.9	2.0–2.2	6½–7
Champasak: (7031)		29.9±5.87	13.8±2.46	2.1±0.07	
Ban Na Deauy, Luang Phrabang: (7036, 7037)	4	22.4–29.4	11.4–13.9	1.8–2.1	6½–7
		26.7±3.32	13.1±1.16	2.0±0.15	
***Amphidromus fuscolabris* Möllendorff, 1898**					
Ban Phone, Sekong:	112	26.0–43.5	13.1–18.1	1.8–2.6	7
(7040, 7041, 7042, 7043)		34.3±3.56	15.2±1.04	2.2±0.13	
Ban Xai Na Pho, Champasak: (7044)	3	26.0–43.6	13.1–18.1	1.8–2.5	7
		34.8±4.06	15.3±1.20	2.2±0.14	
***Amphidromus xiengkhaungensis* sp. nov.**					
Nong Tang, Xieng Khaung: (7045, 7046)	4	21.4–29.8	14.8–17.0	1.4–1.7	6
		25.6±3.49	15.7±1.04	1.6±0.13	

Chapter V

The distribution of terrestrial Pulmonate snails in Laos

Introduction

Land snails are the second most diverse member of phylum Mollusca in term of described species (Lydeard et al., 2004). They are covered over six percent of total invertebrate species on the Earth (Clark and May 2002). However, there are still large number of the tropical molluscan fauna still poorly known while habitat destruction is the major problem so far. They stay as important components in the forest ecosystem by recycling nutrients and are consumed by various kinds of predators such as birds, amphibians, reptiles and other vertebrates including humans (Graveland et al., 1994; Dunk et al., 2004; Deepak et al., 2010).

Pfeiffer (1862), Crosse and Fischer (1863, 1891), Morlet (1892), Ancey (1898); Dautzenberg and Fischer (1905), Panha et al., (2002), Lehmann and Maassen (2004), Maassen (2008) reported a total of 18 families, 50 genera and 92 recognized species from Laos such as Luang Phrabang, Bolikhamxay (Khamkeurt) and Boloven plateau, which are divided into two subclasses: Prosobranchia and Pulmonata. The prosobranchs consist of 4 families10 genera and 16 species, whereas the pulmonates consists of 14 families 40 genera 76 species.

As above information, all collected specimens were recorded on numbers of collected individuals of both adults and juveniles, habitat characteristics, shell height and diameter together with exact localities. The distribution data of Laos's land snails at the family level from three different geographic regions (the northern montane forests, the central limestone karsts, and the south deciduous forests), were recorded for the first time.

The previous studies on taxonomy of pulmonate snails reveal the diversity of 14 families, 40 genera, and 76 species together with the certain recorded localities in Laos by Pfeiffer (1862), Crosse and Fischer (1863, 1891), Morlet (1892), Ancey (1898), Dautzenberg and Fischer (1905), Panha et al., (2002), Lehmann and Maassen (2004), Maassen (2008).

The families Ariophantidae, Camaenidae and Streptaxidae are the major groups containing 10, 7 and 4 genera respectively. Snails occur in various habitats with different ranges of physical environments from low to high altitude. The families Bradybaenidae, Clausiliidae, Diapheridae, Enidae, Euconulidae, Glessulidae, Helicarionidae, Plectopylidae, Subulinidae, Trochomorphidae and Vertiginidae have been classified with one to three genera in each family (Pfeiffer, 1862; Crosse and Fischer, 1863, 1891; Morlet 1892; Ancey, 1898; Dautzenberg and Fischer, 1905; Panha et al., 2002; Lehmann and Maassen, 2004; Maassen, 2008). Those snails occur mostly in the north and central areas at 300 to 1400 m above sea level.

According to literatures, the geographic localities can be divided into three main parts; north, central and south (Joel, 1961). However, most reference specimen labels are written only “Lao Mountains”. These are still problematic for ecological analysis. There are some distinct localities for examples Luang Phrabang, Bolikhamxay (Khamkeurt) and Boloven plateau (Pfeiffer, 1862; Crosse and Fischer, 1863, 1891; Morlet 1892; Ancey, 1898; Dautzenberg and Fischer, 1905).

This study will be an initially analysis on Laos‘s pulmonate snail distribution at the family level based on the current field collecting throughout Laos during September 2013-December 2014.

Materials and Methods

Land snails were sampled from September, 2013 to December, 2014 using direct search technique throughout Laos including the north montane forests, central limestone areas and the south deciduous forests in both national protected areas (NPA) and non-protected areas, anthropogenic areas including the neighboring country borders of China, Vietnam, Cambodia, Thailand and Myanmar. The samples are searched in several microhabitats for examples litter beds, fallen tree trunks, rock surfaces, under the rocks, rock crevices, tree trunks and branches, limestone walls and caves. Hand sorting was applied for collecting samples. The co-ordinations of sampling sites have been recorded by a GPS receiver.

There are 315 localities from 16 provinces and three main recorded parts (Figure 5.1). All living snails and slugs, and all empty shells were collected in each locality. All living snails and slugs were photographed, proceeded to suffocation before preserving in 70% and 95% ethanol. Some specimens were kept in deep freezer at -20 C° for molecular analysis.

Results

Seven teen families, 33 genera and 71 species records from present study, 3 families, 10 genera and 36 species were first time recorded in Laos (Table 5.1). The total 112 species in 50 genera and 17 families of the pulmonate snails were classified from 315 localities throughout Laos. These included with the 76 species from previous studied. As observed from the main snail settlements, three major snail groups have been classified. There are ground dwellers containing 59 species (83%), 11 species (15, 5%) tree dwellers and one species (1.5%) cave dweller (Table 5.1).

The snails in the families Ariophantidae, Camaenidae, Enidae, Helicarionidae and Streptaxidae seem to be major groups which occurring in several habitats from deciduous forest to limestone areas at very wide altitudes from 100 to 1400 m above mean sea level (Figure 5.1).

The families Ariophantidae and Camaenidae perform wide distribution with records of 54 localities containing 36 species from 12 genera (Table 5.1). The genus *Amphidromus* (Camaenidae) exhibits the highest species diversity of eleven, five of *Chloritis* and four of *Camaena* are also recorded, while four species of *Hemiplecta* and three species of *Megaustenia* of Ariophantidae were confirmed. The ranges of distribution of the two families are between latitude 14°–22° N or between altitudes 100-1400 m above mean sea level (Table 5.1).

The following families Bradybaenidae, Clausillidae, Dyakiidae and Trochomorphidae are recorded lesser diverse which occurring in narrow ranges of north and central areas average altitude ranging from 150 to 1400 m above mean sea level (Table 5.1). The major localities are Savannakhet, Khamouan and Bolikhamxay which locate between latitudes 16°–19° N (Figure 5.1).

Interestingly, six are some specific families that found only in the north montane forest at altitude ranging from 300 to 1400 m amsl. They are Diapheridae, Glessuliidae, Plectopylidae, Rathousiidae, Subulinidae and Vertiginidae. The three families: Subulinidae, Vertiginidae and Diapheridae seem to be major groups. The genus *Paraboysidia* (Vertiginidae) is widely distributed which represented by three species, the genus *Prosopeas* (Subulinidae) represented three species, and two in the genus *Sinoennea* (Diapheridae). The specimens were collected from Xiengkhaung, Houaphane, Luang Phrang, Luang Namtha, Oudomxay and Phongsaly Provinces between latitudes 18°–22° N (Figure 5.1).

Discussion

The results have been interpreted that several pulmonate families are sporadically distributed throughout the country. However, when samples from three different geographic areas were compared, the faunal composition between the three areas showed up with different taxa composition.

The north montane forest seems to accommodate twelve families of pulmonate snails, but nine families are recorded in central limestone areas, and six families in the south deciduous forest. The families Ariophantidae, Camaenidae, Enidae, Helicarionidae and Streptaxidae were recorded in all three areas occupying most habitat types, while family Philomysidae is occurred in southern and northern areas (Table 5.1). The genus *Amphidromus* (Camaenidae), the Southeast Asian unique tree snail occupies on various types of trees, because all of their life activities occurring only on the trees, so that the name “tree snail” has been given. The north montane forest and south deciduous forest are the distinct areas for this genus. However, these current undescribed data in southern deciduous forests may reflect the habitat destruction, because the former publications documenting some species such as *Amphidromus haematostoma, A. laosianus* and *A. protania* were listed from Salavan and Champasak provinces. Two pulmonate families are restricted to the northern montane forest between altitudes 330 to 882 m amsl especially the unique microsnails genera *Paraboysidia, Gyliotrachela*, *Krobylos*, *Angustopila* (Vertiginidae) and *Sinoennea*

(Diapheridae). They were recorded from Vangvieng, Luang-Phrabng, Viengxay and Viengphoukha districts (Panha et al., 2002; Maassen, 2008) and Inkhavilay et al., 2016b in Chapter II).

There are nine pulmonate families recorded from central limestone areas. The family Streptaxidae is the major group. The south deciduous forest showing very less diversity with six recorded pulmonate snail families. The most dominant families in the south are Camaenidae and Ariophantidae.

Different types of deciduous forests may only reflect land snail families distribution in Laos, because deciduous forest are less dominant compared to the central and the northern parts. Several studies have been implied that the calcium is positively related to the species richness and density (Burch 1955; Hotopp 2002; Aravind 2005). It is clearly supported why those habitats showed low family's richness than central limestone areas and northern montane forest.

Cryptozona siamensis, *Hemiplecta distincta* and *Achatina fulica* show up wide distribution and abundant which represented the diverse ground dwellers of the Ariophantidae and Achatinidae. This is almost the same pattern as reported in Thailand (Panha, 1987; Panha, 1996; Sutcharit and Panha, 2008; Boonngam et al., 2008; Kulsantiwong et al., 2014). They can be found from low to high altitudes ranging from 116 in the south to 1, 175 m amsl in the north, however, some ariophantids species are endemic and restricted to the type locality, for examples, *Hemiplecta funerea* is confined and endemic to the Viengxay district, Houaphane province, northern of Laos. The specimen is found only at 835 m amsl, while *Sesara bougei* and *S. penoti* are restricted to the limestone out crops of Kao Rao cave, Luang Namtha province at 647 m amsl (Table 5.1).

Amphidromus (Amphidromus) xiengensis shows wide distribution from northern forest at Luang Phrabang to the south deciduous forest at 187 in the south and 539 m amsl at Luang Phrabang. *A. (Amphidromus) roseolabiatus* is confined to central limestone areas up to north montane forest of Luang Phrabang province at 189 in central limestone and 428 m amsl at Luang Phrabang; while *A. (Syndromus) fuscolabris* and *A.* (*Syndromus*) *areolatus* are endemic and restricted to the south deciduous forest. The specimens were collected at Sekong and Attapue provinces at 141 and 206

m amsl respectively. Moreover, *A.* (*Amphidromus*) *syndromoideus* is known only from the type locality and endemic to the central limestone area of Khammouan province at 163 m amsl, and *A.* (*Syndromus*) *xiengkhaungensis* is endemic to the Xiengkhuang province that occurred at 1,140 m amsl (Table 5.1).

The very peculiar Streptaxidae showed up with highly adapted characters of eccentric shells for their living carnivorous habits in specific habitats such as rock crevices, the hollow of soil and under litters (Verdcourt, 2000; Schileyko, 2000; Rowson et al., 2009). The present findings in Laos also confirm the above characters, however, streptaxids were found in only two areas, the north forests and central limestone, karsts from low to high altitudes (143-1,140 m amsl) with high endemism. *Haploptychius porrectus* was found only from Xienkhaung limestones, while *H. pellucens* occurs in very wide ranges in both the northern and central areas. *Perottetia unidentata* found only in the north at Houaphane areas, while *P. megadentata* occurs in the central limestone areas. The two species were found living in different geographic structures and altitudes at 889 m amsl and 163 m amsl, respectively (Inkhavilay et al., 2016a in Chapter III).

There is a notice on the absence of the families Diapheridae, Glessulidae, Plectopylidae, Rathouisiidae, Subulinidae and Vertiginidae in central limestone areas for the families Diapheridae and Vertiginidae are normally restricted and diverse to limestone areas (Jochum et al., 2014). This is quite contradict to the previous reports on two microsnails, *Paraboysidia wangviangensis* and *Krobylos clerxi*, and the five newly described vertiginid and diapherid microsnails in northern limestone areas (Panha et al., 2002; Maassen, 2008; Inkhavilay et al., 2016b in Chapter II). It seems likely that the distribution of Diapheridae and Vertiginidae are restricted to the limestone areas and these animals seem to have the poor dispersal ability.

One possible hypothesis is that of human impacts in the central limestone areas making habitat destructions such as limestone quarries, intensive land uses, logging business, animal hunting and dam construction. I have also noticed that the larger animals such as small reptiles, birds and small mammals are difficult to find but it is quite usual to see its at local morning markets in both living and dead materials.

The species list of pulmonate snails found from the present study and the previous records showing the high diversity which similar to the close area such as Thailand in term of taxa composition (Table 5.1). However, there are almost double in species records for Thailand. It is because of the accumulation from the thirty years of research from fundamental taxonomy to advance systematics (Panha, 1996; Sutcharit and Panha, 2006; Sutcharit and Panha, 2008; Sutcharit et al., 2010a; Siriboon et al., 2013; Siriboon et al., 2014a, b; Sutcharit et al., 2015). There will be some further attempt to make the official inventory in the near future for Laos terrestrial snails in both pulmonates and operculates taxa.

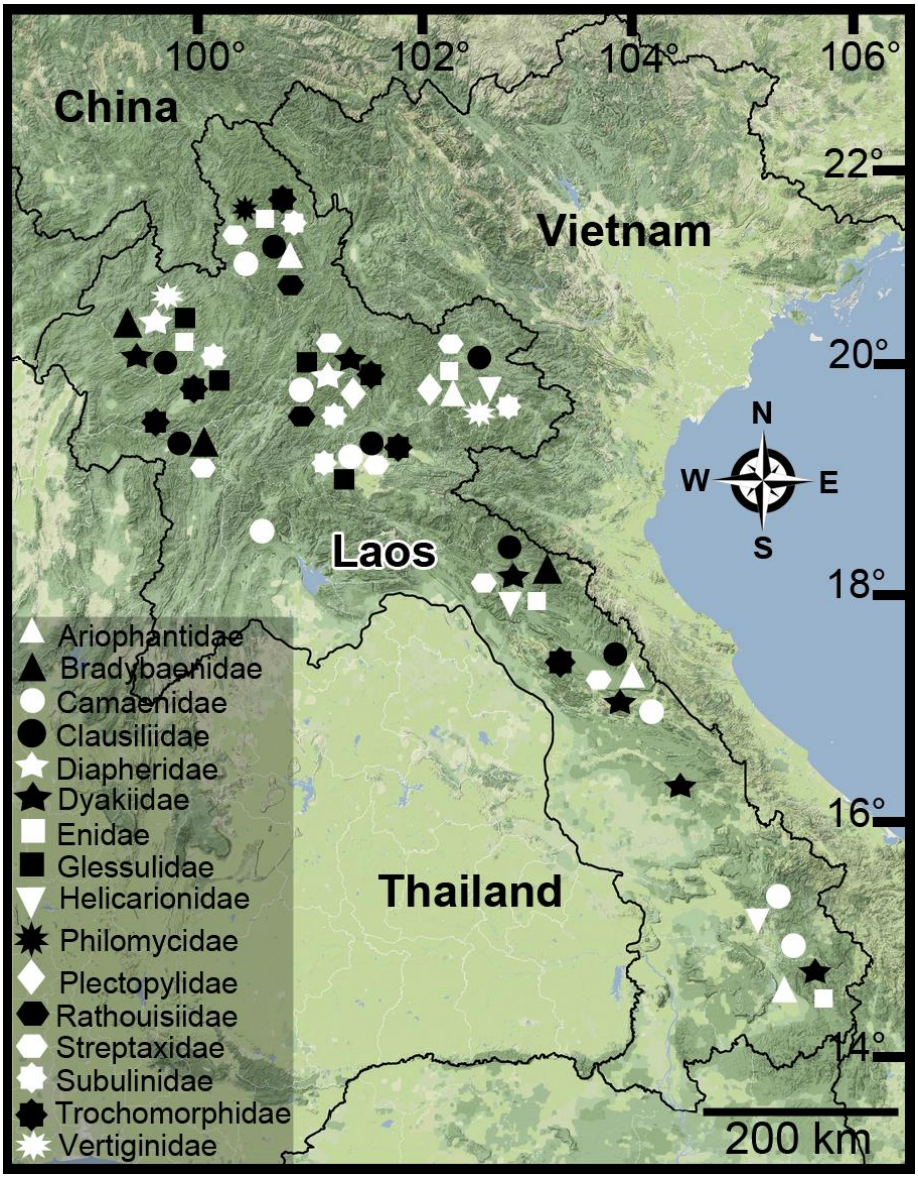

Figure 5.1 Distribution map of the pulmonate snail families in Laos from this study.

Table 5.1 The pulmonate land snail families collected in different parts and altitudes in Laos. (✓) = presence; (–) = absence, (*) = Previous records.

Families/genera/species	Geographical regions			Elev. (m)
	Northern	Central	Southern	
1. Ariophantidae Godwin-Austen, 1888				
(1). *Cryptozona siamensis*	✓	✓	✓	116–335
(2). *Sesara bougei*	✓	–	–	647
(3). **S. penoti*	✓	–	–	647
(4). *Durgella libas*	✓	–	–	350-687
(5). **Hemiplecta distincta*	✓	✓	✓	175-1, 175
(6). **H. pluto*	✓	✓	–	163-177
(7). *H. esculenta*	✓	–	–	429
(8). *H. funerea*	✓	–	–	835
(9). **Macrochlamys callojuncta*	✓	–	–	351
(10). *Megaustenia siamensis*	–	–	✓	969-1, 199
(11). *M. maleticus*	✓	–	–	858
(12). *Megaustenia* sp.	✓	–	–	539
(13). *Parmarion* sp.	✓	✓	✓	367-906
(14). *Sarika resplendens*	✓	–	–	539
(15). *Sarika* sp.	✓	–	–	345
2. Achatinidae Swainson, 1840				
(16). *Achatina fulica*	✓	✓	✓	116–335
3. Bradybaenidae Pilsbry, 1934				
(17). *Aegista coudeini*	–	✓	–	480
(18). **Bradybaena tenella*	–	✓	–	650
4.Camaenidae Pilsbry, 1895				
(19). *Amphidromus (A.) roseolabiatus*	–	✓	✓	189-428
(20). *A. (A.) givenchyi*	–	–	✓	364
(21). **A. (A.) laosianus*	–	–	✓	N.A.
(22). *A. (A.) pervariabilis*	✓	–	–	834
(23). **A. (A.) protania*	–	–	✓	N.A.

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Table 5.1. The pulmonate land snail families collected in different parts and altitudes in Laos. (✓) = presence; (–) = absence, (*) = Previous records (Continued).

Families/genera/species	Geographical regions			Elev. (m)
	Northern	Central	Southern	
(24). *Amphidromus (A.) syndromoideus*	–	–	✓	163
(25). *A. (Syndromus) areolatus*	–	–	✓	141
(26). **A. (S.) flavus*	✓	✓	–	299-314
(27). *+*A. (S.) fuscolabris*	–	–	✓	206
(28). **A. (S.) xiengensis*	✓	✓	✓	187-539
(29). *A. (S.) xiengkhaungensis*	✓	–	–	1, 140
(30). *Camaena choboensis*	✓	–	–	1, 248
(31). **C. illustris*	✓	–	–	647-1, 466
(32). *C. subratosca*	–	✓	–	177
(33). *C. vanbuensis*	✓	–	–	899-1, 466
(34). **Chloritis deleciosa*	✓	–	–	855
(35). *C. diplochone*	✓	–	–	172
(36). *C. balansi*	✓	–	–	687
(37). *C. durandi*	–	✓	–	341
(38). *C. fouresi*	✓	–	–	304
(39). *Möllendorffia hariola*	✓	–	–	330
5.Clausiliidae Gray, 1855				
(40). **Causilia dautzenbergi*	–	✓	–	504
6. Diapheridae Panha & Naggs, 2010				
(41). **Sinoennea lizae*	✓	–	–	687
(42). *S. euryomphala*	✓	–	–	330
7. Dyakiidae Gude & Woodward, 1921				
(43). **Quantula weinkauffiana*	–	✓	–	189-428
(44). *Quantula* sp.	–	✓	–	143
8. Enidae Woodward, 1903				
(45). **Coccoderma corti*	✓	✓	✓	143-1, 466

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Table 5.1. The pulmonate land snail families collected in different parts and altitudes in Laos. (✓) = presence; (–) = absence, (*) = Previous records (Continued).

Families/genera/species	Geographical regions			Elev. (m)
	Northern	Central	Southern	
9.Glessulidae Godwin-Austen, 1920				
(46). **Glessula paviei*	✓	–	–	732
(47). *G. latectrita*	✓	–	–	732
10. Helicarionidae Bourguignat, 1877				
(48). **Helicarion maleficus*	✓	✓	✓	472-718
11. Philomycidae Gray, 1847				
(49). *Philomychus* sp.1	✓	–	–	1, 466
(50). *Philomychus* sp.2	–	–	✓	978
12. Plectopylidae Möllendorff, 1898				
(51). **Chersaecia laomontana*	✓	–	–	427
(52). *Chersaecia* sp.	✓	–	–	695
13. Rathouisiidae Heude, 1885				
(53). *Atopos sarasini*	✓	–	–	335
14. Streptaxidae Gray, 1860				
(54). **Haploptichius pellucens*	✓	–	–	504-732
(55). **H. porrectus*	✓	–	–	608-1, 140
(56). *H. blaisei*	✓	–	–	330
(57). *Perrottetia aquilonaria*	✓	–	–	409-878
(58). *P. unidentata*	✓	–	–	889
(59). *P. megadentata*	–	✓	–	163
(60). *Indoartemon tridens*	–	–	✓	N.A.
(61). *I. diodonta*	–	✓	–	143-163
15. Subulinidae Fischer & Crosse, 1877				
(62). *Allopeas henrici*	✓	–	–	1, 466
(63). *Prosopeas excellens*	✓	–	–	330
(64). *P. ventrosulum*	✓	–	–	1, 140
(65). *P. tunicula*	✓	–	–	1, 140

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Table 5.1. The pulmonate land snail families collected in different parts and altitudes in Laos. (✓) = presence; (–) = absence, (*) = Previous records (Continued).

Families/genera/species	Geographical regions			Elev. (m)
	Northern	Central	Southern	
16. Trochomorphidae Möllendorff, 1890				
(66). *Trochomorpha paviei*	–	✓	–	174
17. Vertiginidae Fitzinger, 1833				
(67). *Paraboysidia gittenbergeri*	✓	–	–	687
(68). *P. anguloobtusus*	✓	–	–	732
(69). *P. paralella*	✓	–	–	732
(70). *Gyliotrachela plesiolopa*	✓	–	–	695
(71). *Angustopila singuladentis*	✓	–	–	882

Chapter VI
The cladistics analysis in the Ariophantidae

Introduction

The Family Ariophantidae Godwin-Austen, 1888 categorized into three superfamilies; **Limacoidea, Arionoidea and Helicoidea** (Bouchet and Rocroi, 2005) which are usually distributed along **tropical and subtropical areas** such as **Indian territory** and south-eastern Asia (Hausdorf, 2000). This land snail family contains enormous diversification and several members in this groups are also categorized into three shell morphological/biological characteristics; snail, slugs and semi-slugs. Currently, the classification and identification of family Ariophantidae are based on the morphological characters of shell and **reproductive system** (Blanford and Godwin-Austen, 1908; Godwin-Austen, 1907 (1882-1920); Schileyko, 2002a; Solem, 1966). There are several proposed genera of this family that nowadays still showing up complicated unrelated characters which making classification problematic such as in the two related genera *Macrochlamys* and *Sarika* (Abu-Bakar et al., 2014) which are classified in the subfamily Macrochlamydinae. Up to now, a very good cladistic studies on land snails has been conducted in the family Dyakiidae using shell characteristics and genital characters by Hausdorf in 1995.

To resolve those problem, the initial phylogenetic tree among members in the family Ariophantidae was reconstructed based on shell morphology and reproductive organ characteristics. Eight species from 5 genera collected from Laos and Thailand were used in this study. The relationship of selected genera will be analyzed and compared with previous classification hypotheses of the Ariophantidae, that we expecting to add up a new discussion on ariophantid snails.

Material and Methods

The 29 traditional characters of Ariophantidae were selected in this analysis (Table 6. 2). Five genera ingroup and one outgroup from the Camaenidae were selected for cladistic analysis. Five genera of family Ariophantidae such as *Cryptozona, Hemiplecta, Megaustenia, Sarika* and *Macrochlamys* were included in this study. The matrix of morphological characters was made in Mesquite (Maddison and Maddison, 2009), and calculated by TNT (Goloboff et al., 2008b). The morphological characters for analysis were mostly modified and followed Hausdorf (1995). The character matrix includes 29 characters from shell, genital system and radula is shown in Table 6.1.

Cladistics analysis

In equal-weights analysis, tree yield was gathered from traditional search using 100 random sample replications with additional TBR branch swapping based on 10 starting trees. The sampling frequencies were tested from 1,000 replicates of jack-knife test for evaluating the support value of node splitting and symmetric re-sampling with the probability of character removal that set to 0.36.

Equal weight analysis

Parsimony analysis with equal weight yielded one short tree of 48 steps (consistency index (CI) = 0.436, retention index (RI) = 0.102).

The statistical support (Jack-knife and systematic resampling) for the branches is generally weak. The most homoplastic characters are character 5 (flagellum), 8 (ectocone of radula marginal teeth) and 28 (shell thick or thin). The tree were rooted between *Camaena illustris* and the rest.

The ingroup is the best supported branch on the tree; therefore, the analysis support *Hemiplecta* as a paraphyletic group.

The base of the ingroup consists of basal "ladder": (*Hemiplecta distincta*+ *(Hemiplecta pluto*+ *(Cryptozona siamensis*+ clade 3 and 4, consist of 5 taxa.

Comments on selection clade

For brevity, the terminal taxa are referred by the genus name only. The clade are indicated on the tree (Figure 6.1).

Results

The genus *Hemiplecta*

Two selected members of this genus, namely *H. distincta* and *H. pluto* represent ambiguous relationship either monophyletic or paraphyletic as indicated from clade splitting between this two congeneric members. *H. distincta* was separated from other selected taxa by three synapomorphies: central tooth monocuspid (**character 7: 0**); shell width or shell width more than 20 mm (**character 12:1**); aperture height more than 20 mm (**character 14:1**) and umbilicated umbilicus (**character 17:3**). However, *H. distincta* separates from *H. pluto* by only one character: missing of ectocone of marginal teeth radula (**character 8: 2**).

The cladistics analysis was clarified as follows:

Clade1 *Cryptozona+Macrochlamys+Sarika+Megaustenia*

Monophyly of this group is indicated by six synapomorphies: central tooth tricuspid (**character 7: 2**); shell width less than 40 mm (**character 12: 1**); aperture height less than 20 mm (**character 14: 0**); aperture width less than 25 mm (**character**

15: 0); spire height less than 10 mm (**character 16: 0**) and shell thin and strong (**character 28: 1**).

Clade 2 *Cryptozona+Macrochlamys+Sarika*

This clade gathering three common land snail genera in Southeast-Asia; *Cryptozona, Macrochlamys* and *Sarika.* This clade depicted monophyletic relation that was indicated by two synapomorphies characters: long flagellum (**character 5: 0**) and number of radula teeth per row with less than 200 (**character 9: 0**).

Clade 3 *Macrochlamys+Sarika*.

This clade relationship depicts monophyly which was supported by two syapomorphies characters: sculpture present only growth line (**character 23: 0**) and vagina length short and stout (**character 26: 1**). Moreover, *Sarika* is distinguished from *Macrochlamys* by four synapomorphies characters: present of mantle flap (**character 20: 0**); shell polished (**character 22: 0**); apparatus dart position lower than penis (**character 27: 1**) and shell thin and weak (**character 28: 2**).

Clade 4 *Megaustenia*

Monophyly of the genus is supported by four syapomorphies characters: showing long epiphallus (**character 1: 0**); number of whorls more than 2 (**character 10: 2**); shell covered by mantle (**character 21: 0**) and aperture with subcircular shape (**character 29: 0**).

Discussion

The relationships within the family Ariophantidae have been evaluated in broad-scale sampling based on observation of traditional taxonomic protocol (Godwin-Austen, 1907; Schileyko, 2002b; 2003). In this study, the cladrogram indicated the selected members of Ariophantidae that occur in Southeast-Asia represents monophyletic relationship. The data matrix that gathered from taxonomic character for recent generic and specific identification protocol such as shell characteristics, radula teeth characters and genital system.

Eight selected species from 5 genera of the family Ariophantidae have been sampled to calculate the cladogram. The separation of Ariophantidae members from the outgroup *Camaen*a (Camaenidae) was strongly supported by 100 % bootstrap value (Figure 6. 1). In the Ariophantidae, the genus *Hemiplecta* showned unsettled position. Two selected species are not united. *H. distincta* was placed as basal clade of other Ariophantidae members including *H. pluto*. The ectocone of radula marginal teeth (character 8:2) scored as missing in *H. distincta* is the significant character to separate *H. pluto* from *H. distincta*; two selected *Hemiplecta* forming paraphyly with low bootstrap value (44%). However, the external morphological characters that can be used to distinguish these two species are shell characteristics and the coloration of soft body (Pfeiffer, 1863a).

The results strongly support separating other genera from *Hemiplecta* by having smaller shell. This was supported by bootstrap value 98%.

The long flagellum and radula teeth per row less than 200 are strongly support separating *Cryptozona* + *Macrochlamys* + *Sarika* from the genus *Megaustenia*.

The growth line on shell sculpture and short and stout vaginal shape are significant characters that support separating *Macrochlamys* and *Sarika* from the genus *Cryptozona*.

The mantle flap and polished shell are absent in *Macrochlamys* and in most genera except *Sarika.* Those characters suggest the taxonomic classifying and strongly support *Sarika* separating from *Macrochlamys*, but the two genera are still superficially very close relationship and the classification is often confused, but as the new results appeared the two genera should not be retained in the same genus. However, the relationship between two closely related genera still ambiguous according to lower statistical support (69%). This result is congruent with previous works which also conduct based on molecular and morphological classification (Abu-Bakar et al., 2014). They suggest that *Sarika* belongs to the subfamily *Macrochlamydinae* (Figure. 6.1).

The initial relationships between members of Ariophantidae still showing ambiguity according to the cladistics result. To clarify and emendate the classification hypothesis of this land snail family, some representative genera and species are needed for both the morphological and molecular analyses. The further surveys in some more details of genital system is also required.

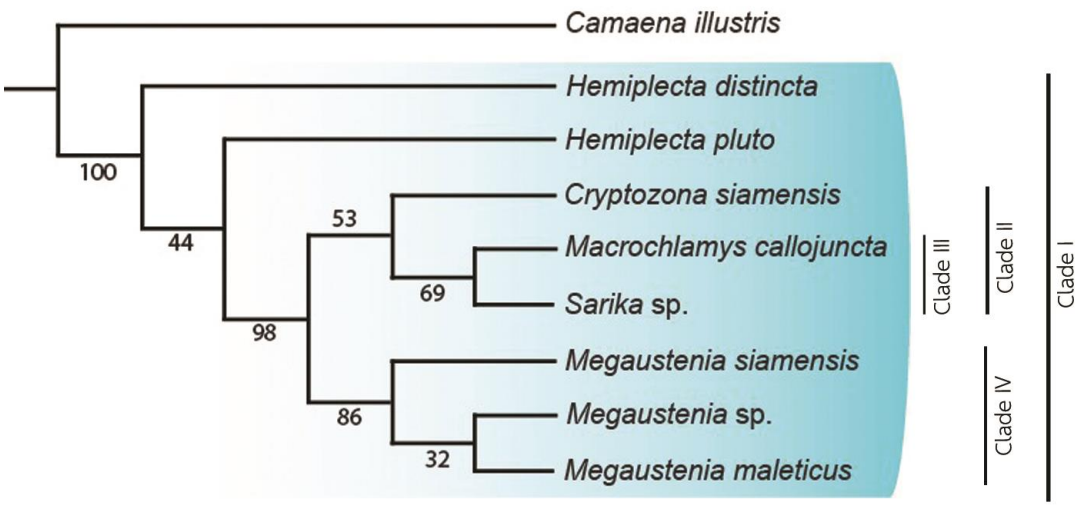

Figure 6.1 Phylogenetic of relationships between members of the Ariophantidae: Equally-parsimonious tree of length 48 (CI = 0.436, RI = 0.102) from parsimony analysis weight.

Table 6.1 Character matrix of 29 morphological characters

Taxa	Characters		
	0000000001	1111111112	222222222
	1234567890	1234567890	123456789
Cryptozona siamensis	101?001101	0000001001	1111?0010
Hemiplecta distincta	101?001101	0111113001	111100000
Hemiplecta pluto	101?100011	0111113001	111000000
Sarika sp.	101?001001	0000001000	100001120
Megaustenia maleticus	001?001110	0001000000	011000011
Meguastenia sp.	001?101110	0010000001	011000011
Megaustenia siamensis	001?101010	0000000001	011001111
Macrochlamys callojuncta	1000000001	0000001001	110011010
Camaena illustris	111?110201	1111110211	111110?02

Table 6.2 Characters used in the phylogenetic analysis

(1)	Epiphallus: 0 = long; 1 = short
(2)	Epiphalic caecum: 0 = present; 1 = absent
(3)	Spermatophore: 0 = present; 1 = absent
(4)	Spermatophore: 0 = thick walled; ? = unknown
(5)	Flagellum: 0 = long; 1 = short; ?= unknown
(6)	Dart: 0 = with dart; 1 = without dart.
(7)	Central tooth: 0 = monocupid; 1 = tricupid
(8)	Ectocone of radula marginal: 0 = very small ; 1 = medium; 2 = absent
(9)	Number of radula teeth per row (in brackets actual number): 0 = less than 200; 1 = more than 200
(10)	Number of whorls (in brackets actual number): 0 = more than 2; 1 = more than 4
(11)	Body whorl: 0 = rounded or angled; 1= keeled
(12)	Shell width (in brackets actual breadth in mm): 0 = less than 40 mm; 1 = (usually) more than 40 mm
(13)	Shell high (in brackets actual high in mm): 0 = less than 25 mm; 1 = more than 25 mm
(14)	Aperture high (in brackets actual high in mm): 0 = less than 20 mm; 1 = (usually) more than 20 mm
(15)	Aperture width (in brackets actual breadth in mm): 0 = less than 25 mm; 1 = (usually) more than 25 mm
(16)	Spire high (in brackets actual high in mm): 0 = less than 10 mm; 1 = (usually) more than 10 mm

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Table 6.2 Characters used in the phylogenetic analysis (Continued).

(17)	Umbilicus: 0 = imperforate; 1 = perforate; 2 = rimately perforate; 3 = umbilicate
(18)	Aperture: 0 = aperture expanded not reflected; 1 = aperture lip expanded; 2 = aperture lip reflected
(19)	Foot sole: 0 = present; 1 = absent
(20)	Mantle flap: 0 = present; 1 = absent
(21)	Mantle covered shell: 0 = present; 1 = absent
(22)	Shell : 0 = polished; 1 = not polished
(23)	Shell sculpture: 0 = growth line; 1 = growth line and striae
(24)	Protoconch: 0 = smooth; 1 = not smooth
(25)	Penis sheath: 0 = present; 1 = absent
(26)	Vagina: 0 = long and cylindrical; 1 = short and stout
(27)	Base of penis and dart: 0 = same position; 1 = dart lower;? Unknown
(28)	Shell: 0 = thick; 1 = thin and strong; 2 = thin and weak
(29)	Aperture shape: 0 = subcircular; 1 = circular; 2 = semioval

Chapter VII

Discussion and conclusion

Laos terrestrial pulmonate snail fauna has long been investigated and considered to contain less diversity with 14 families 40 genera and 76 species (Pfeiffer, 1862; Crosse and Fischer, 1863, 1891; Morlet, 1892; Ancey, 1898; Pilsbry, 1900; Dautzenberg and Fischer, 1905; Laidlaw and Solem, 1961, Richardson, 1985, Panha et al., 2002; Lehmann and Maassen, 2004; Sutcharit and Panha 2006; Maassen 2008; Schileyko 2011). In the present study, 112 species have been discovered. These included with the 76 species from previous studied with ten newly described making over a hundred recognized species (Inkhavilay et al., 2016 a, b, c in Chapter II, III, IV and Table 5.1 in Chapter V). The species composition is not so impressive when comparing with about 600 Thai species and 400 Vietnamese species (Panha, 1996; 1997; Panha and Burch, 1999a, b, 2000, 2001; Sutcharit and Panha, 2008; Sutcharit et al., 2010b; Siriboon et al., 2013, 2014a, b; Sutcharit et al., 2015; Schileyko, 2011).

However, the 43 species native to Laos (see Table 5.1 in Chapter V) are slightly more than expectation, and some species are even very remarkable to the region for examples the tree snails *Amphidromus (Amphidromus) roseolabiatus*, *A. (Amphidromus) pervariabilis, A. (Amphidromus) givenchyi*; the carnivorous streptaxids, *Haploptichius blaisei* and *Perrottetia aquilonaria*, *Perrottetia unidentata,* and the microsnails, *Paraboysidia anguloobtusus, P. paralella, Gyliotrachela plesiolopa*, *Angustopila singuladentis*, *Sinoennea euryomphala* (Inkhavilay et al., 2016 a, b, c in Chapter II, III and IV).

Diversity in the three different geographic regions

Laos is the only landlocked country in Southeast Asia, and it locates between latitudes 14° and 23°N, and longitudes 100° and 108°E, with the total area 236,800 km^2. Ecologically, it has been divided into three distinct regions: the north montane forest, the central limestone karsts and the south deciduous forest (Joel, 1961). The northern areas showed up with slightly diverse for land pulmonate snails than other regions. The tree snails genus *Amphidromus* appeared in many mountainous areas which are

now in threatened condition because of the main reason on forest destruction for examples *Amphidromus* (*Amphidromus*) *roseolabiatus* and *A. (Syndromus) flavus* at Luang Prabang. The ground snail family Ariophantidae are very diverse with almost 8 genera and 15 species (see Table 5.1 in Chapter V). This is reflect to habitat diversity in the northern region. It is very popular that some land snail species are used as food for examples *Hemiplecta distincta* and the operculate snail genus *Cyclophorus.* It was mentioned that those two snail types are consumed and exported to Thailand more than one million snails per year. The northern area also contains some limestone outcrops but mostly being quarried, however, some unique microsnails were described in this study for examples *Paraboysidia anguloobtusus* found from Luang Namtha, *P. paralella* from Luang Namtha, *Gyliotrachela plesiolopa* from Houaphane, the first species of the genus ever recorded in Laos, *Angustopila singuladentis* from Houaphane, the species also is the first species of the genus recorded in Laos and *Sinoennea euryomphala* from Luang Prabang. The carnivorous snails family Streptaxidae, two species of *Perrottetia* and one *Indoartemon* were found as newly described species in both north and central areas, *Perrottetia unidentata* from Houaphane, *P. megadentata* from Khammouan central area and *Indoartemon diodonta* from Khammouan (Inkhavilay et al., 2016a in Chapter III).

The carnivorous Streptaxidae and Diapheridae

The Streptaxidae Gray, 1860 and Diapheridae Panha and Naggs, 2010 are the families of carnivorous snails that are very endemic to mostly limestone karsts. The Southeast Asian streptaxids and diapherids show up with the unique shell eccentric structures but tiny with cylindrical shell shapes in Diapheridae, with specific apertural dentitions, and the remarkable yellowish to orange body color (Zilch, 1960; Schileyko, 2000; Rowson et al., 2010a, b; Siriboon et al., 2013, 2014a, b). The four genera were formerly recorded in Laos, *Discartemon* Pfeiffer, 1856, *Perrottetia* Kobelt, 1905, *Haploptychius* Möllendorff, 1906, and *Indoartemon* Forcart, 1946. There are eight species in total records for Lao territory. Three newly described species: *Perrottetia unidentata, P. megadentata* and *Indoartemon diodonta* have been discovered in this

present study from the northern and central areas which contain many limestone outcrops (Inkhavilay et al., 2016a in Chapter III). In this study, *Perrottetia* shows wide range distribution both in the north and central areas while *Indoartemon* has specific area in central limestones, however, *I. tridens* (Mollendorff, 1898) was reported from Champasak in the southern area. I have made several attempts in searching at Champasak in 2013 and 2014, but failed. There may be because of habitat destruction recently. So, in this current conclusion, we still believe that the Streptaxidae and Diapheridae are limited to limestone habitats. The soft body characters are very helpful for identification. Radula teeth and internal sculpture of genitalia such as penial and vaginal hooks are so clear to distinguish species so that the three new species have been confirmed.

The ground dwellers Ariophantidae

Lao people know land pulmonate snails by encountering with mostly ground dwellers such as the dominant *Cryptozona siamensis* and *Hemiplecta distincta* two species were found in all three regions, but *C. siamensis* occurs in mostly in anthropogenic areas but less in natural forest. This is probably because the snails are predated by many animals from firefly larvae, birds and small mammals. It is quite often to find broken shells in many areas. *Hemiplecta distincta*, the edible snails of the region livinge in sandy dipterocarp forest, consume various kinds of fungus including the toxic species like *Amanita* (Panha, 1987). In this present study *H. distincta* specimens were collected in three regions at various altitudes up to thousand meters above the sea level while *Cryptozona siamensis* occurs only at low altitudes (see Table 5.1 in Chapter V). There are three endemic *Hemiplecta* found, *H. esculenta, H. funerea* and *H. pluto.* These three species seem to not occur in Thailand. There are also some genera of semi slugs occur in many areas such as *Parmarion* sp. but *Megaustenia siamensis* the dominant larger and wide distributed Thai semi slug species was found only in the southern area of Laos. The shell and genital characters are interesting because it is almost problematic to identify some genera by shell characters

such as *Sarika*; several genital and radula characters are still the significant characters for identification (Sutcharit and Panha, 2008).

Distribution of pulmonate snail families in Laos.

The ground dweller Ariophantidae and the tree dweller Camaenidae occur in almost all of habitat types in Laos. *Cryptozona siamensis*, *Hemiplecta distincta* and *Achatina fulica* have wide distribution and quite dominant taxa occuring in Laos. This result shows similar pattern with the previous reports of those genera found in Thailand (Panha, 1987, 1996; Sutcharit and Panha, 2008; Boonngam et al., 2008; Kulsantiwong et al., 2014). The Ariophantidae are known as common snails that occurring in various habitats in many tropic countries such as India, south-eastern Asia, Eastern Asian tropics and Australia (Hausdorf, 2000; Cuezzo, 2003; Sutcharit and Panha, 2008).

Amphidromus (Syndromus) xiengensis is widely distributed, the animals represented in both south deciduous forest and northern montane forest. *A. (Amphidromus) roseolabiatus* occurs only in central limestone areas and northern montane forest, but *A. (Amphidromus) pervariabilis* and *A. (Syndromus) xiengkhaungensis* are restricted to northern areas (Morlet, 1891; Fulton, 1896 and Inkhavilay et al., 2016c in Chapter IV). The distribution pattern of *Amphidromus* in Laos is almost similar to the reports for Thai species (Panha, 1996; Sutcharit and Panha, 2006; Sutcharit et al., 2015; Inkhavilay et al., 2016c in Chapter IV).

The second dominant taxa are the Bradybaenidae, Clausilliidae, Streptaxidae, Dyakiidae and Trochomorphidae. They confined to limestone areas in the central and northern limestone especially the Streptaxidae represented in both the central and northern areas. This family seems to confine to limestone areas. However, this is quite contradict to Streptaxidae distribution pattern as reported in neighboring country such as in Thailand. They can be found in limestone areas in the south such as Ranong up to northern limestone karsts areas at Chiang Mai province (Siriboon, 2013; Siriboon, 2014a, b).

The above mentioned on distribution may not be answered the questions perfectly because less sampling sites have been surveyed in this study. There are still

many areas remain to be critically sampled in different seasons but rainy season need to be concentrated. And for better understanding real biodiversity, the comparative studies with the former papers of the nearby countries such as Thailand and Vietnam are also needed to be concentrated. Therefore, more cumulative surveys are only the way for better understanding of the terrestrial pulmonate snail diversity and distribution in Laos.

The morphological relationships among ariophantid members

Because the dominant ground dwellers in the family Ariophantidae are so diverse in shell characters and soft bodies. There are two types of snail in this family, the snails and the semi-slugs. It seems like they are mostly separated from each other perfectly so that the generic classification has been completely done. The several genera such as *Cryptozona, Hemiplecta, Megaustenia, Parmarion* and *Sarika* are quite different from each other in shell characters and genital organs. However, there are still some close affinities in some genera for examples *Macrochlamys* and *Sarika*, and genital organs are very similar in some genera. The morphological cladistics analysis result of eight species from five genera revealed monophyletic arrangement but still unsettled and the bootstrap supports in some clades are low. *Hemiplecta distincta* was placed in the basal but slightly separated from *H. pluto. Cryptozona, Macrochlamys* and *Sarika* are arranged in the same clade. The present of mantle flap and polished shell characters make *Sarika* separating from *Macrochlamys* and even from other genera. The initial molecular analysis on some Malaysian ariophantid by Abu-Bakar et al. in 2014 also interpreted the similar result. The semi-slugs *Megaustenia* are placed in very clear separated clade. It is supported the animals that are transforming from snails to slugs as seen from the rudiment shell characters.

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APPENDIX

VITA

Mr. Khamla Inkhavilay was born on May 2nd, 1975 in Houaphane province, Laos.

His interest in invertebrates began during the invertebrate's class at Department of Biology, Faculty of Education, National University of Laos. He received his bachelor's degree in education major on the General Biology in 1998.

Then, he decided to start working on Laotian earthworm's taxonomy and also began to intend Master degree in field of Zoology at Department of Biology, Faculty of Natural Science, National University of Laos, and finished his Master degree with the thesis entitled "The morphological of earthworm genus Amynthas at Nam-Et Phouleoi Houaphane province and Dong Hua Sao National protected area in Champasak province Laos P. D. R." in 2013. During the course of his graduate studies, he gave a lecture for undergraduate courses on invertebrates, including earthworms and land snails in general and received main responsibility for the arrangements of field trips and partial teaching.

Subsequently, he decided to work on land snail's taxonomy in Laos, inspired by Prof. Dr. Somsak Panha. He was granted with the CU-ASEAN scholarship for the doctoral degree and started intending a Zoology program at the Department of Biology, Faculty of Science, Chulalongkorn University since 2013.