

# NEW AND LITTLE-KNOWN CLAUSILIIDAE (GASTROPODA: PULMONATA) FROM LAOS AND SOUTHERN VIETNAM

BARNA PÁLL-GERGELY<sup>1</sup> & MIKLÓS SZEKERES<sup>2</sup>

<sup>1</sup>Department of Biology, Shinshu University, Matsumoto 390–8621, Japan

<sup>2</sup>Institute of Plant Biology, Biological Research Centre of the Hungarian Academy of Sciences, Temesvári krt. 62, H-6726 Szeged, Hungary

*Abstract* Recently collected materials held at the Musée National d'Histoire Naturelle (Paris) yielded important new information on the Clausiliidae of Laos and Vietnam. The data considerably increase and refine the hitherto scarce knowledge on the distribution of the *Garnieria Bourguignat*, 1877 and *Grandinenia Minato & Chen*, 1984 species of Laos, and reveal a new Vietnamese subgenus, *Garnieria (Doducsangia) subgen. nov.* (type species: *Garnieria mouhoti nhuongi Do*, 2015). From the Hon Ba Nature Reserve of Vietnam's Khanh Hoa Province *Oospira naggsi parva subsp. nov.*, *Castanophaedusa fontainei gen. nov. sp. nov.*, and *Messageriella gargominyi gen. nov. sp. nov.* are described as new taxa. The zoogeographical significance of these findings is discussed.

*Key words* Garnieriinae, Phaedusinae, taxonomy, new taxa, zoogeography

## INTRODUCTION

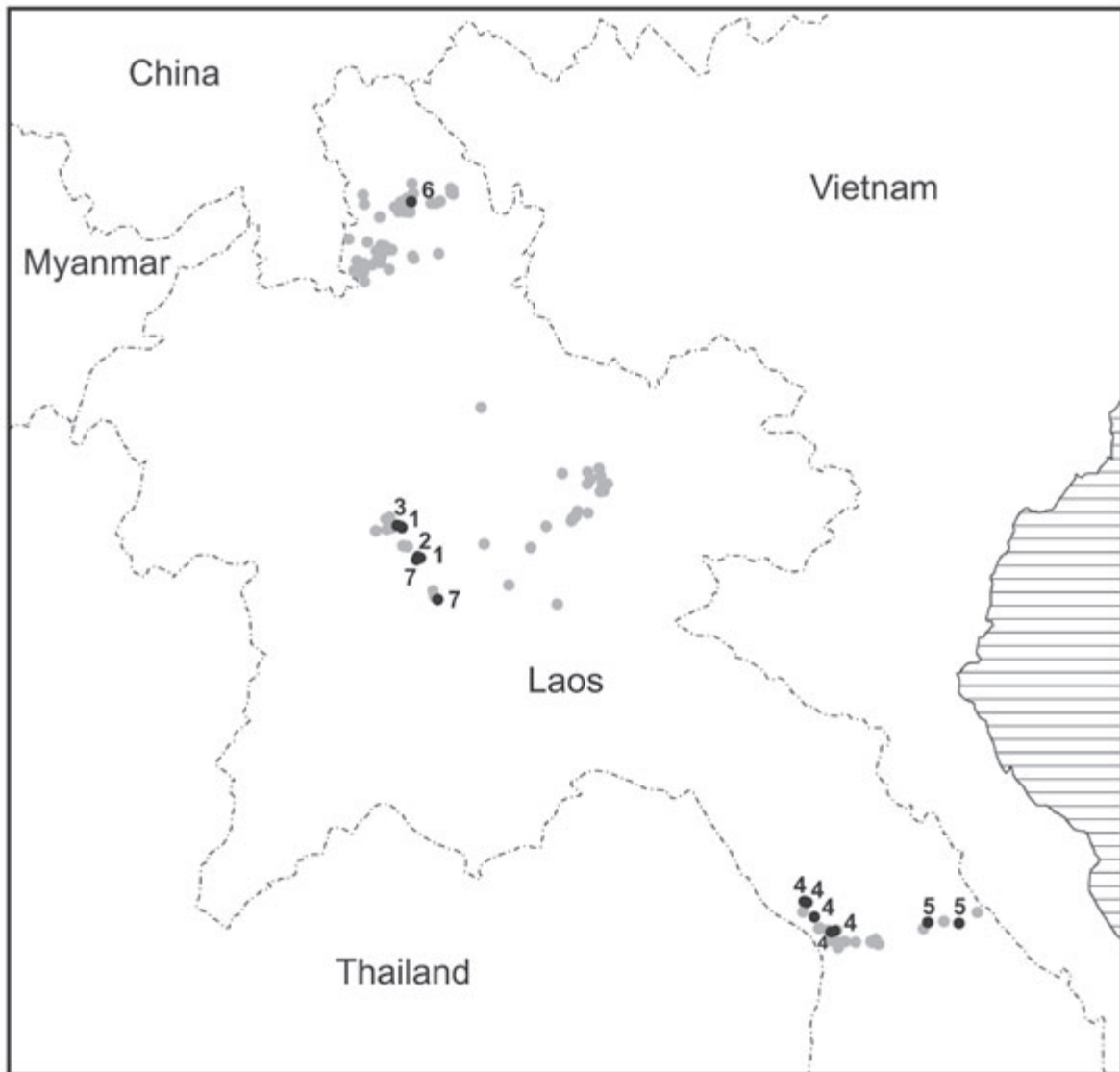
Compared to the historically well-researched northern areas of Vietnam (see assessed in Schileyko, 2011), the Clausiliidae fauna of southern Vietnam and Laos is quite poorly known. In addition to the pioneering publications of Pfeiffer (1841, 1862), Morlet (1892) and Möllendorff (1898), the clausiliids of these regions have been dealt with only in a few recent publications (Nordsieck, 2002a, 2003, 2012; Grego & Szekeres, 2011; Grego *et al.*, 2014; Nguyen, 2016). During the past two decades, however, intensified ecological and biodiversity surveys in Southeast Asia yielded valuable new materials that made possible to expand our knowledge on the fauna of its uniquely rich forestlands.

The present study is based on clausiliid samples of the Musée National d'Histoire Naturelle (Paris) that have been collected during field trips to Khammouan, Luang Prabang and Phongsaly Provinces in Laos, as well as Khanh Hoa Province in Vietnam. Ethanol-preserved specimens from these collections, and also one from Vietnam's Son La Province, allowed anatomical study and taxonomic evaluation of some little-known and newly discovered species. The results obtained, together with new distribution data, give a substantially refined view of the diversity and environmental constraints of the Clausiliidae fauna in these areas.

## MATERIALS AND METHODS

The studied material from Laos was obtained from Khammouan, Luangprabang and Phongsaly Provinces during three biodiversity surveys, which were carried out by Ahmed Abdou and Igor V. Muratov from 2005 to 2007 in the frameworks of the Eco-Valley Program (supported by the governments of the Centre Region in France and the Province of Luang Prabang) and the "Chaines annamitiques" project of the Musée National d'Histoire Naturelle, Paris. The sampling sites of these field trips are shown in Fig. 1. Mainly empty shells were recovered from layers of leaf litter and top soil samples. The clausiliids from Vietnam were collected by Benoit Fontaine and Olivier Gargominy as part of a 2013 field study at the Hon Ba Nature Reserve (Fig. 2), funded by the LabEx BCDiv biodiversity program of the Museum National d'Histoire Naturelle (Paris) and supported by the Institute of Tropical Biology (Ho Chi Minh City).

Radula samples were prepared by solubilising the attached soft tissues in 2 M KOH and subsequent washing in 70% ethanol. The obtained preparations and the clausilium plates of small-size species were imaged directly under low vacuum using a Miniscope TM-1000 scanning electron microscope (Hitachi, Tokyo). In descriptions of the genital organs proximal and distal positions are given in relation to the gonads.



**Figure 1** Map of Laos showing all collection sites of the 2005 to 2007 MNHN expeditions (grey and black dots) and those where Clausiliidae species were found (black dots): *Garnieria* (*G.*) *mouhoti* (Pfeiffer) (1), *Garnieria* (*G.*) *mouhoti* (Pfeiffer) together with *Margaritiphaedusa* sp. (2), *Garnieria* (*G.*) *mouhoti* (Pfeiffer) together with *Margaritiphaedusa* sp. and *Phaedusa micropaviei* Nordsieck (3), *Grandinenia dautzenbergi* (Morlet) (4), *Grandinenia tonkinensis* Nordsieck (5), *Oospira abstrusa ginkae* Grego & Szekeres (6), and *Margaritiphaedusa* sp. (7).

The type material mentioned in the text is housed in the collections of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (SMF), Musée National d'Histoire Naturelle, Paris (MNHN), Natural History Museum, London (NHMUK), and the Naturalis Biodiversity Centre, Leiden (NBC).

#### SYSTEMATICS

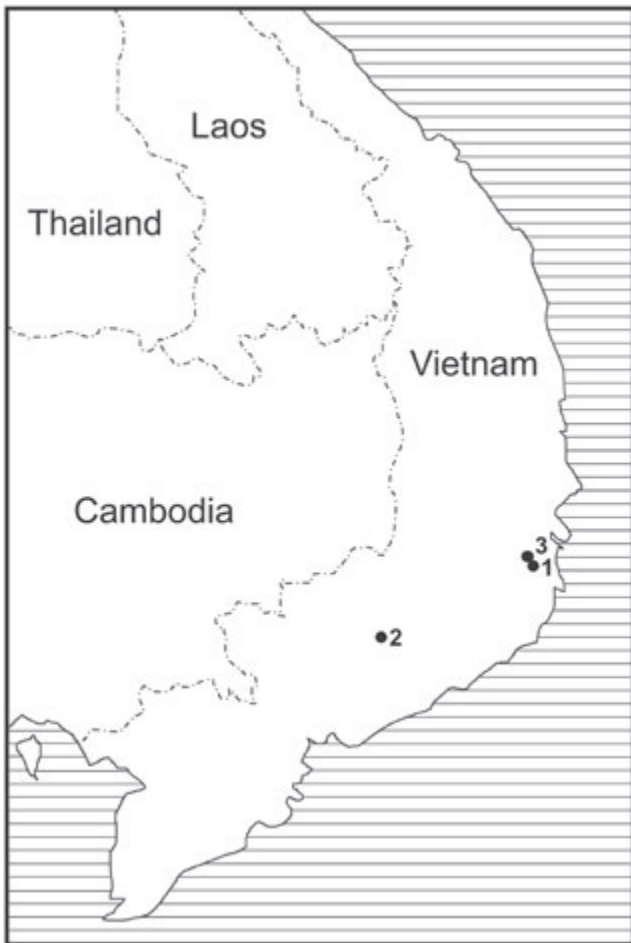
Family CLAUSILIIDAE

Subfamily GARNIERIINAE

#### *Garnieria* Bourguignat, 1877

Type species: *Clausilia mouhoti* Pfeiffer, 1862;  
OD.

The genus is comprised of three subgenera. The nominotypical subgenus, known from northern Laos and China's Yunnan Province, includes *G. (G.) mouhoti* Pfeiffer and *G. (G.) saurini* Nordsieck, 2012. *Garnieria* (*Progarnieria*) Nordsieck, 2012 of northern Laos and *G. (Doducsangia)* subgen. nov. of northwestern Vietnam are represented only by their respective type species, *G. (P.) huleschheliae*



**Figure 2** Map of southern Vietnam showing the type localities of *Oospira naggsi parva* subsp. nov., *Castanophaedusa fontainei* sp. nov., *Messageriella gargominyi* sp. nov. (1), *Oospira naggsi naggsi* Luong & Szekeres (2), and *Castanophaedusa huberi* (Thach) (3).

Grego & Szekeres, 2011 and *G. (D.) nhuongi* Do, 2015.

***Garnieria (Garnieria)* Bourguignat, 1877**

*Garnieria (Garnieria) mouhoti* (Pfeiffer, 1862)  
(Figs 3a, c, 4a–b, e–g, 5)

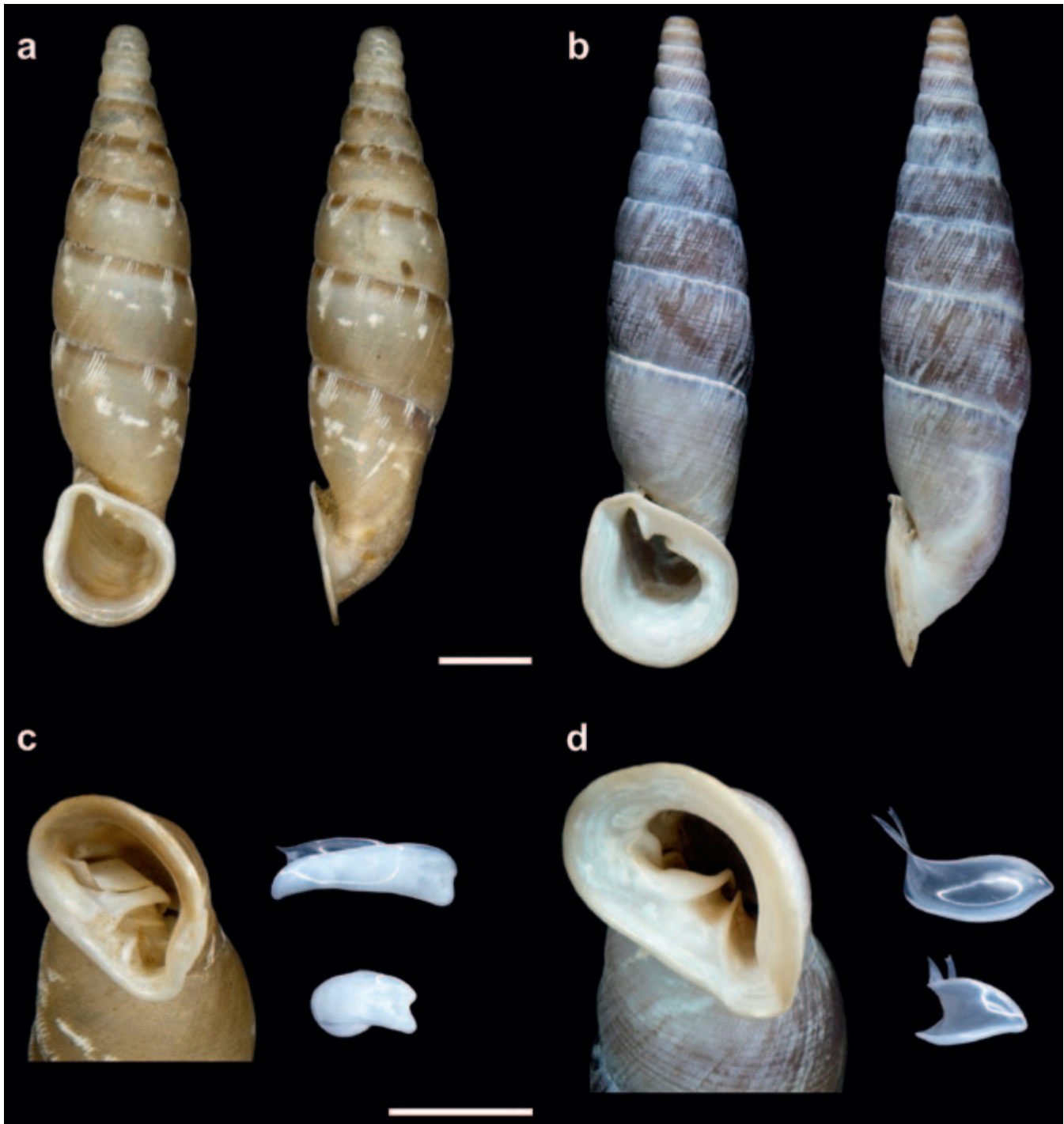
The taxonomic status of this species was assessed by Nordsieck (2002a). He studied the type material of *Clausilia mouhoti* (NHMUK 20010206, from the “Lao Mountains, Camboja”, but likely the vicinity of Luang Prabang in Laos) and of *Clausilia massiei* Morlet, 1892 (MNHN-IM-2000–2509, from “Luang Prabang”), being a junior synonym of *G. (G.) mouhoti*, as well as samples from Luang Prabang (leg. C. Roebelen) and Ban Huai Tong (19°53' N 102°04' E) in the immediate vicinity of

Luang Prabang (leg. R. Brandt). More recently this species has also been found in Mengla Xian of China’s Yunnan Province (Nordsieck, 2012; Chen, 2016).

The newly available material of *G. (G.) mouhoti* (all from Laos, Luang Prabang Province) was collected at the following localities (Fig. 1): 18km SE of Muang Xiang Ngeun, left side of the Nam Khan River (19°40'55.9" N 102°19'44.6" E, 460m), leg. A. Abdou & I. V. Muratov 30.10.2006 (MNHN-IM-2012–27180, dry; MNHN-IM-2012–27181 to -27183, ethanol-preserved) (non-decollated form); 17km SE of Muang Xiang Ngeun, left side of the Nam Khan River (19°41'12.1" N 102°19'11.8" E, 390m), leg. A. Abdou & I. V. Muratov 30.10.2006 (MNHN-IM-2012–27184, dry; MNHN-IM-2012–27185, ethanol-preserved) (non-decollated form, found together with *Margaritiphaedusa* sp.); 9km SE of Luang Prabang, left side of the Nam Khan River (19°51'22.9" N 102°12'27.4" E, 370m), leg. A. Abdou & I. V. Muratov 03.11.2006 (MNHN-IM-2012–27188, dry) (decollated form); Mt. Phou Xuang, 1.5km NE of Ban Lak Sip, 5km SE of Luang Prabang (19°51'36.3" N 102°11'04.9" E, 640m), leg. A. Abdou & I. V. Muratov 24.11.2006 (MNHN-IM-2012–27190, dry) (decollated form, found together with *Margaritiphaedusa* sp. and *Phaedusa micropaviei*).

Intriguingly, even in the immediate vicinity of Luang Prabang some of the populations are decollated, whereas others possess intact shells. In fact, the shell characters in each of the above four populations differ noticeably from those of the others. The observed variation is in the same range as those between the nominotypical subspecies, *G. (G.) m. moellendorffi* Nordsieck, 2002, and *G. (G.) m. yunnancola* Nordsieck, 2012 (= *Tropidauchenia mengyuanensis* Chen, 2016, syn. nov.) (Nordsieck, 2002a, 2012; Chen, 2016). Considering the substantial inter-population variability, it is not clear whether any subspecific division could be meaningful with the current limited knowledge of this species.

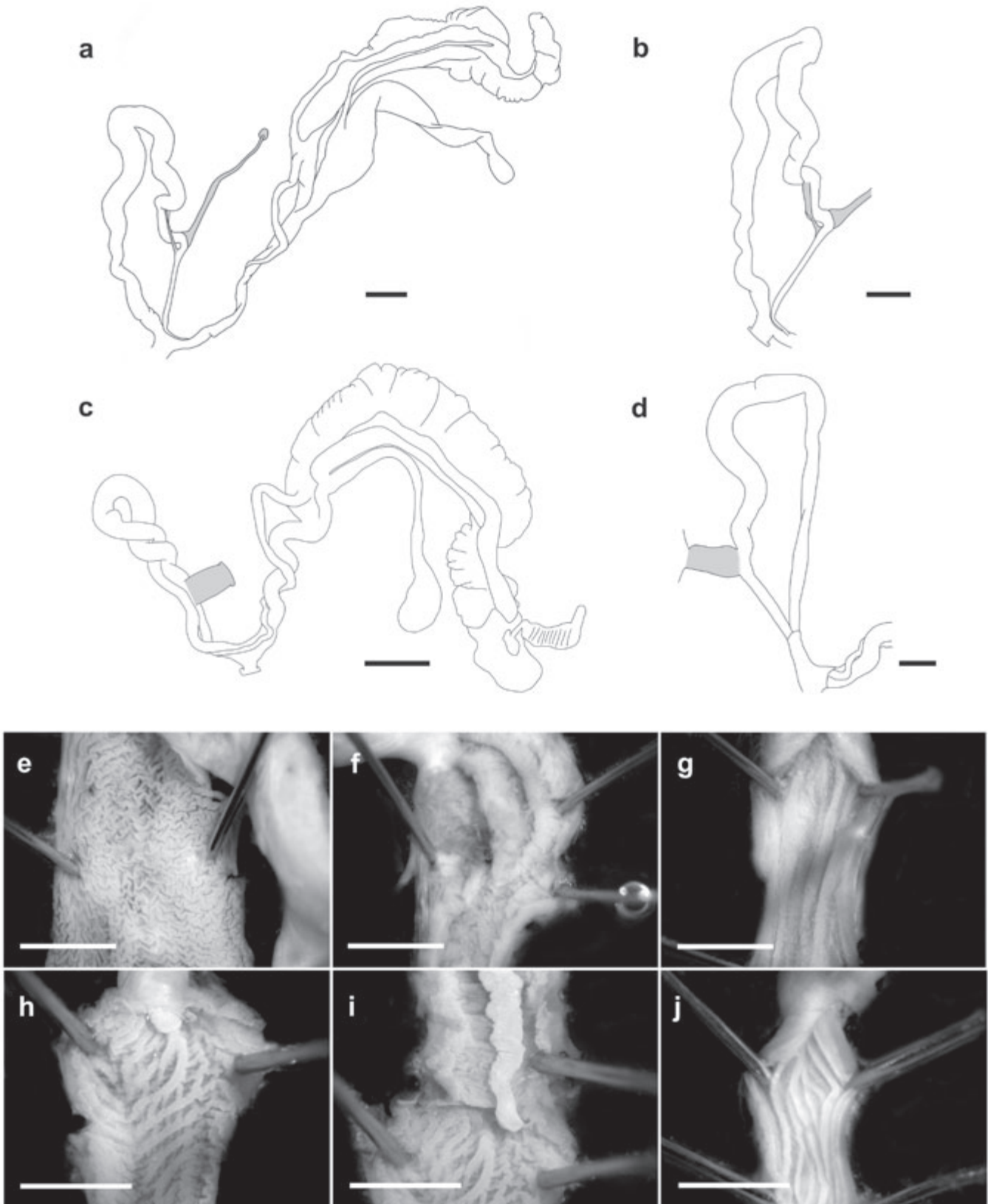
The ethanol-preserved specimens (MNHN-IM-2012–27181 and -27182) made possible the examination of the genital anatomy, which differs substantially from those of other *Garnieriinae* genera. Most prominently, whereas in the male part the retractor muscle is attached to the penis in *Megalauchenia* Nordsieck, 2007 (Szekeres, 1969; Loosjes & Loosjes-van Bommel, 1973);



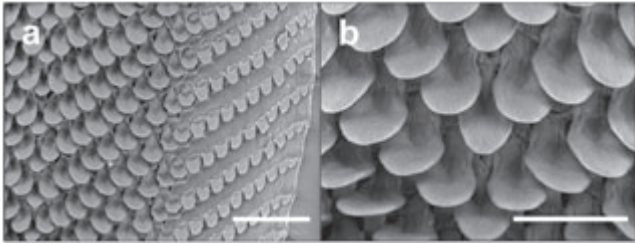
**Figure 3** *Garnieria (G.) mouhoti* (Pfeiffer) from Laos, Luang Prabang (a, c) and *Garnieria (Doducsangia) nhuongi* Do, paratype (b–d). Shells (a, b) and apertures with clausilium plates (c–d). Scale bars represent 5mm.

*Grandinenia* Minato & Chen, 1984 (Szekeres, 1998; Minato, 1992) and *Ptychauchenia* Nordsieck, 2010 (Nordsieck, 2010), in *Garnieria (G.) mouhoti* its attachment is at the epiphallus (Fig. 4a–b). The penis and the thicker epiphallus are of similar lengths, from the outside their transition is not easily recognizable. Inside the penis has a dense

reticulate pattern (Fig. 4e), while the lumen of the epiphallus is partitioned by three strong longitudinal folds (Fig. 4f). The retractor muscle is broadly attached to the epiphallus near its proximal end. A small, distinct auxiliary muscle connects two points of the proximal epiphallus, which are distal and proximal to the retractor



**Figure 4** Reproductive organs of *Garnieria (G.) mouhoti* (Pfeiffer) (a–b, e–g) and *Garnieria (Doducsangia) nhuongi* Do (c–d, h–j). General morphology of the organs (a–d), and internal structures of the penis (e, h), penis to epiphallus transition (f, i), and the vagina (g, j). Scale bars represent 2mm (a, c) and 1mm (b, d–j).



**Figure 5** Radula of *Garnieria (G.) mouhoti* (Pfeiffer). Central to marginal (a) and central to first three lateral teeth (b). Scale bars represent 200 (a) and 100  $\mu\text{m}$  (b).

attachment site (Fig. 4b). The vagina is about as long as the penis, inside it has several longitudinal crinkles (Fig. 4g). The pedunculus of the bursa copulatrix is robust. It is widest at the entrance of the very thin diverticulum, which is as long as the distal pedunculus. The proximal pedunculus is somewhat longer, with a slightly widened, ovoidal bursa at its end (Fig. 4a).

The radula is very similar to those of other *Garnieriinae* genera. It consists of V-shaped tooth rows, in which half rows meet at an angle of roughly  $120^\circ$ . The central tooth and on both sides nine lateral teeth of similar size are spade-shaped with rounded cusps, whereas the 11 marginals become gradually smaller and rhomboidal toward the edges (Figs 5a–b).

#### *Garnieria (Garnieria) saurini* Nordsieck, 2002

This relatively small, decollated species was described on the basis of a single specimen (holotype, MNHN-IM-2000–2672) that had been collected by E. Saurin in Laos, “Pah Xieng Tong, Pah Hia” (Nordsieck, 2002a). The location most likely corresponds to Ban Namthong ( $18^\circ 59' \text{N}$   $103^\circ 16' \text{E}$ ) in the Pah Xieng Tong mountain range, Vientiane Province (Páll-Gergely, Muratov & Asami, 2016).

#### *Garnieria (Doducsangia)* subgen. nov.

Type species: *Garnieria mouhoti nhuongi* Do, 2015

*Differential diagnosis* The diagnostic characters of the new subgenus are those of the type species.

*Etymology* The new genus is named after Do Duc Sang of the Tay Bac University (Quyet Tam, Son La Province, Vietnam), who described the type species and kindly provided material for this study.

#### *Garnieria (Doducsangia) nhuongi* Do, 2015 (Figs 3b, d, 4c–d, h–j)

*Differential diagnosis* *Garnieria (D.) nhuongi* differs from all other *Garnieria* species by its strong and very long lamella superior, well emerged lamella inferior, almost entirely reduced lamella inserta, and its deep positioned, pointed clausilium plate (Fig. 3d).

The species has been well described in Do & Do (2015). The following extension is based on ethanol-preserved specimens (MNHN-IM-2012–27210 and -27211) received from the type locality (Vietnam, Son La Province, Phu Yen District, Muong Do,  $21^\circ 11' 46'' \text{N}$   $104^\circ 47' 06'' \text{E}$ ).

The clausilium plate (Fig. 3d) widens gradually from the base to about two thirds of its length, then it terminates in a moderately pointed tip. The central part is strongly bent along the axis. By contrast, the clausilium plate of *G. (G.) mouhoti* (Fig. 3c) widens abruptly at its base, and then has roughly equal width until its blunt, somewhat recessed end.

The main arrangement of the genital organs (examined in two specimens) is similar to that seen in *G. (G.) mouhoti*. The penis and the wider epiphallus are of comparable lengths. At their border a rudimentary caecum is visible (Figs 4c–d). The inner wall of the penis has a strong reticulate structure (Fig. 4h), whereas that of the epiphallus forms a strong longitudinal ridge that extends somewhat into the lumen of the proximal penis (Fig. 4i). The penial retractor is attached broadly at the proximal epiphallus, which has no auxiliary muscle. Around the atrium the vas deferens is bound to the distal ends of the penis and the vagina by strong ligaments. The vagina is of the same length as that of the penis. Its inner wall has several longitudinal folds (Fig. 4j). The pedunculus of the bursa copulatrix is about as thick as the diverticulum. Its distal part is much shorter than the proximal one, which has comparable length to that of the diverticulum. The ovoidal bursa is considerably wider than its pedunculus (Fig. 4c). The radula structure is the same as in *G. (G.) mouhoti*.

Despite the basic similarity, the genital organs of *G. (D.) nhuongi* also show conspicuous differences from those of *G. (G.) mouhoti*. Unlike in that species, the single strong fold of the epiphallus reaches over into the penial lumen, the proximal epiphallus has no auxiliary muscle, the

diverticulum is not much thinner but as thick as the proximal pedunculus. These features, together with the shell characters that distinguish *G. (D.) nhuongi* from all other species of the genus, seem to support separation at the subgeneric level. Whereas the three subgenera of *Garnieria* show differences that indicate evolutionary distances larger than those between species, the common morphological characters that clearly distinguishing them from other genera of the Garnieriinae position them in the same genus. Molecular phylogenetic data indicate that the evolution of *Garnieria* diverged from those of other genera in the subfamily (exemplified by *Grandinenia*) quite early, about 21.9 million years ago. This event is estimated to pre-date the divergence of European and Asiatic members of the subfamily Phaesusinae (Uit de Weerd & Gittenberger, 2013).

*Grandinenia* Minato & Chen, 1984

Type species: *Steatonenia mirifica* Chen & Gao, 1982; OD.

*Grandinenia* includes several species inhabiting areas from the western edge of China's Guangdong Province to southern Laos (Hunyadi & Szekeres, 2016). Nordsieck (2016) classifies the Laotian and some Vietnamese species of the genus in *Neniauchenia* Nordsieck, 2002 (type species: *Clausilia rugifera* Möllendorff, 1898), which he originally described as a subgenus of *Tropidauchenia* Lindholm, 1924 (Nordsieck, 2002a). In our view, however, these species are closest related to *G. ardouiniana* (Heude, 1885) of northeastern Vietnam, and the diagnostic shell characters of *Neniauchenia* mentioned by Nordsieck (2002a) are all within the variability ranges of the *Grandinenia* species (Grego *et al.*, 2014). Whereas the classification of all these species within *Grandinenia* still needs molecular confirmation, our assessment is strongly supported by the apparent agreement of the genital structures (Szekeres, 1998; Grego *et al.*, 2014).

*Grandinenia amoena* (Nordsieck, 2002)

This species was described on the basis of material that had been collected by Edmond Saurin in Laos. The holotype (MNHN-IM-2000-2410) originates from "Phou Tiou" (Nordsieck 2002a),

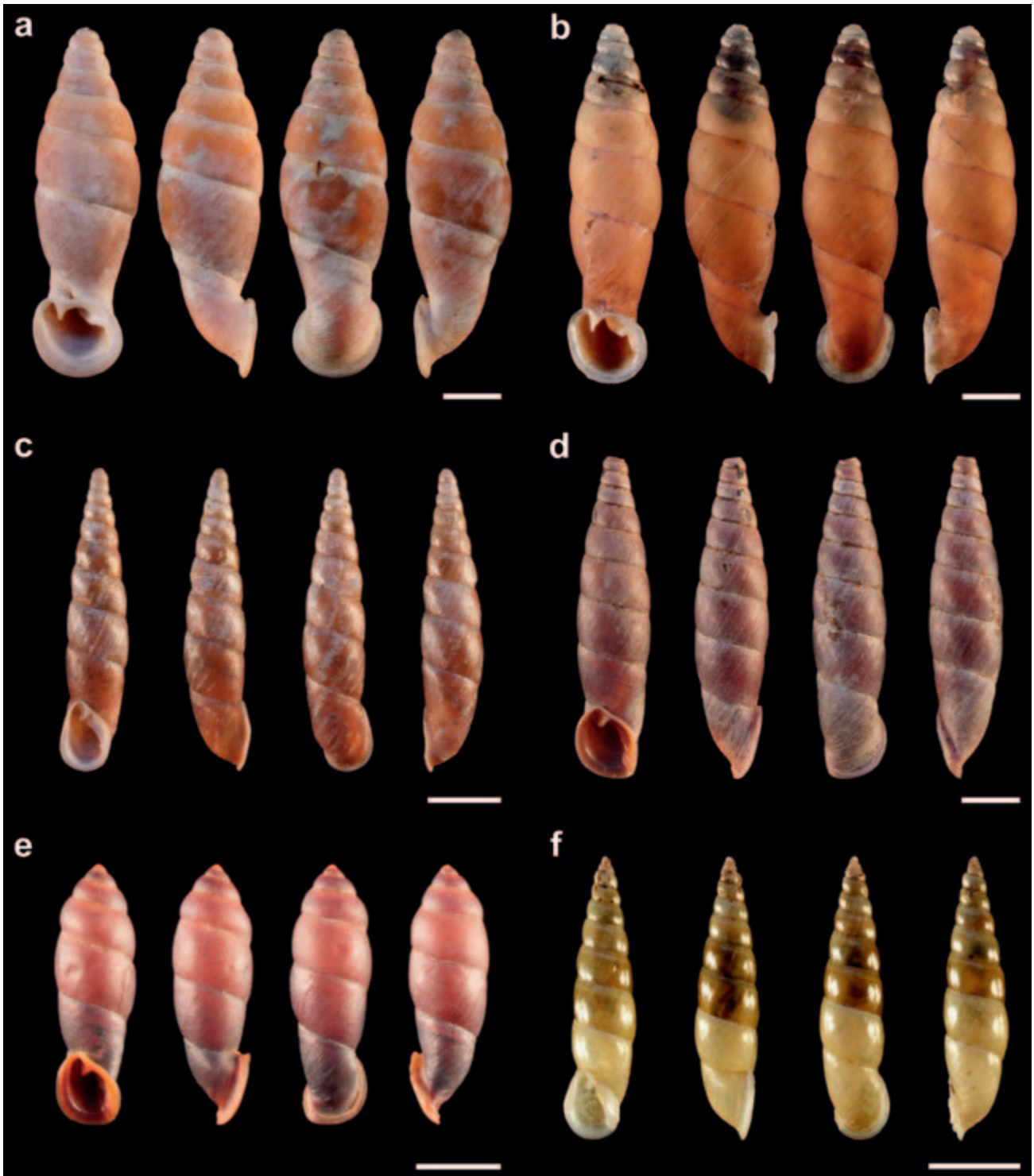
which most likely corresponds to Phon Tiou (also spelled Phom Tiu; at 17°53'56" N 104°35'36" E), an important mining site in Khammouan Province. Paratypes are available from "Ban Peng", likely referring to Ban Houei Pi Peng (Khammouan Province, 17°51'05" N 104°39'26" E) near the type locality. Recently *G. amoena* has been found at Nakai (Khammouan Province, 17°35'09.1" N 105°10'18.2" E, 180m, leg. A. Reischütz), about 70km SE of Phon Tiou. Another sample was collected by F. Huber near Thakhek (Khammouan Province).

The corroded type material made it questionable whether *G. amoena* is an extant species (Nordsieck 2002a). However, the new samples contain fresh fallen shells with bright ochre whorls that are separated by a purple-brown suture band. The neck is also purple-brown, with darker streaks along the plica principalis and the lunella.

*Grandinenia dautzenbergi* (Morlet, 1892)  
(Fig. 6a)

This species (syntypes: MNHN-IM-2000-2432) has been described from "Kham-Keute", that is the Khamkeut District (18°11' N 104°57' E) in Laos, Bolikhamsai Province. The subspecies *G. d. decollata* Nordsieck, 2002 (holotype: MNHN-IM-2000-2433), differing from the typical *G. dautzenbergi* only by its decollation and deeper lunella (Nordsieck, 2002a), was described from "B. (= Ban) Na Ka Yak", corresponding to Ban Na Cadac/Na Kayak (17°28'28" N 105°07'48" E) in Laos, Khammouan Province.

The newly available material of *G. dautzenbergi* is from the following localities (all in Laos, Khammouan Province; Fig. 1): 16km NE of Thakhek (Muang Khammouan), 2.3km ESE of Ban Nase (17°30'49.7" N 104°54'20.3" E, 160m), leg. A. Abdou & I. V. Muratov 28.11.2007 (MNHN-IM-2012-27193, dry); 34km WNW of Thakhek (Muang Khammouan) (17°40'49.3" N 104°42'02.3" E, 140m), leg. A. Abdou & I. V. Muratov 03.12.2007 (MNHN-IM-2012-27194, dry); 33km WNW of Thakhek (Muang Khammouan), 8.5km ENE of Ban Namdik (17°40'39.2" N 104°42'49.6" E, 160m), leg. A. Abdou & I. V. Muratov 03.12.2007 (MNHN-IM-2012-27195, dry); 12.5km NE of Thakhek (Muang Khammouan), 3km SW of Ban Nase (17°29'50.5" N 104°51'58.3" E, 190m), leg. A. Abdou & I. V. Muratov 04.12.2007



**Figure 6** *Grandinenia dautzenbergi* (Morlet), Laos, Khammouan Province, 16km NE of Thakhek (a); *Grandinenia tonkinensis* Nordsieck, Laos, Khammouan Province, 4km W of Ban Phong Dong (b); *Oospira naggisi parva* subsp. nov., holotype, MNHN-IM-2012-27205 (c); *Castanophaedusa fontainei* sp. nov., holotype, MNHN-IM-2012-27207 (d); *Castanophaedusa huberi* (Thach), Vietnam, Khanh Hoa Province, Khanh Vinh District, Yang Bay Waterfalls (e); *Messageiriella gargominyi* sp. nov., holotype, MNHN-IM-2012-27208 (f). Scale bars represent 5mm.

(MNHN-IM-2012-27196, dry); 22km NNW of Thakhek (Muang Khammouan), 5.5km NNE of Ban Nakok, 7km ESE of Ban Namdik

(17°35'13.4" N 104°45'58.8" E, 170m), leg. A. Abdou & I. V. Muratov 08.12.2007 (MNHN-IM-2012-27200, dry).



The subspecific status of *G. d. decollata* is questionable, because it differs from the studied material only by its slight decollation. The deeper positioned lunella, also mentioned as diagnostic feature in the description (Nordsieck, 2002a), can also be seen in the recently collected shells from the Thakhek region.

*Grandinenia tonkinensis* (Nordsieck, 2010)  
(Fig. 6b)

*Grandinenia tonkinensis* (holotype: SMF 331370) has been known from a few localities in Vietnam's Quang Binh Province (Nordsieck, 2010). Its type locality was erroneously given as the "Cuc Phuong N. P." in Ninh Binh Province (Nordsieck, 2010), and later corrected as likely the Phong Nha-Ke Bang National Park of Quang Binh Province (Grego *et al.*, 2014; Nordsieck, 2016).

The newly available material (all from Laos, Khammouan Province) is as follows (Fig. 1): 4km W of Ban Phong Dong, less than 1km S of Road 12, across the river Houei Ine (17°34'20.9" N 105°38'36.6" E, 190m), leg. A. Abdou & I. V. Muratov 06.12.2007 (MNHN-IM-2012-27197 and -27198, dry); 8.5km WSW of Ban Xieng Dao, just NW of Road 12 (17°34'24.2" N 105°27'08.7" E, 210m), leg. A. Abdou & I. V. Muratov 06.12.2007 (MNHN-IM-2012-27199, dry).

Conchologically this species is very similar to *G. dautzenbergi* (Fig. 6a–b), from which it differs merely by its more elongate shell and the slightly forward-bent, non-fused basal end of the lunella. Recently collected samples from the assumed type locality (Grego *et al.*, 2014; Nordsieck, 2016) show that, in contrast to the description (Nordsieck, 2010), the shell is not decollated.

Subfamily PHAEDUSINAE

*Oospira* Blanford, 1872

Type species: *Clausilia philippiana* Pfeiffer, 1847;  
OD.

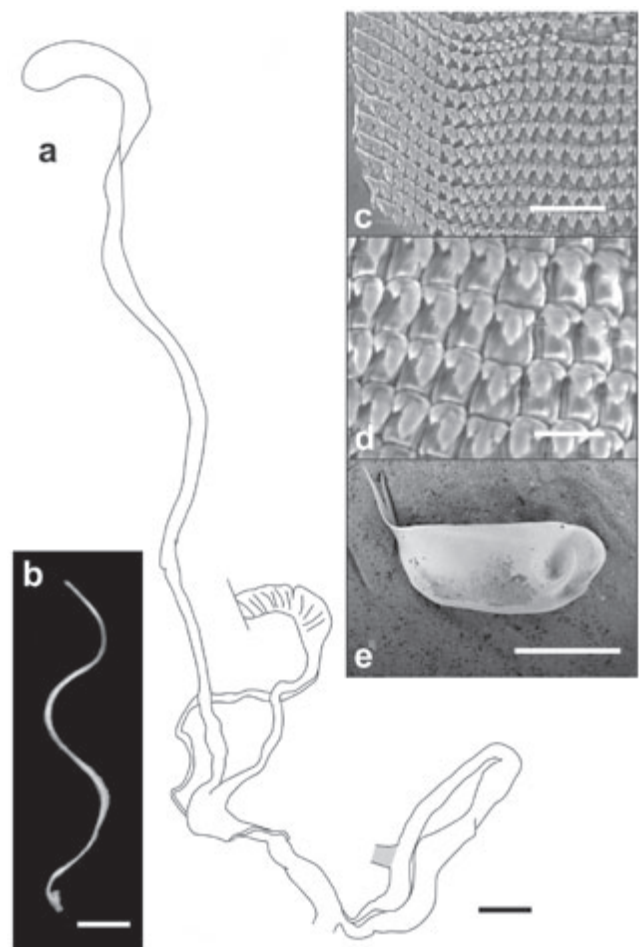
*Oospira abstrusa* Szekeres, 1970

The nominotypical subspecies of *O. abstrusa* was described from the Cuc Phuong National Park, which is divided between Ha Nam, Hoa Binh and Ninh Binh Provinces of Vietnam, whereas type locality of *O. a. ginkae* Grego & Szekeres, 2014 is Tay Trang in Vietnam's Dien Bien Province, near its border with Laos.

*Oospira abstrusa ginkae* Grego & Szekeres, 2014  
(Figs 7a–e)

This subspecies was collected by Abdou and Muratov in Laos, Phongsaly Province, along the northeastern ridge of the Phoufa Mts, NE of Phongsaly (21°43'09.4" N 102°7'44.7" E, 920m) (Fig. 1). The live collected specimens (MNHN-IM-2012-27178 and -27179, ethanol-preserved) made possible a detailed morphological study of this clausiliid.

From one of the specimens the clausilium was removed and examined. Its weakly bent plate gradually widens from its basis before narrowing and terminating abruptly in a rounded tip. On the outside of the plate, at its widest part, a strong hook was observed that emerged from the parietal and bent toward the columellar side (Fig.



**Figure 7** *Oospira abstrusa ginkae* Grego & Szekeres: genital organs (a), spermatophore (b), central to marginal (c) and central to first two lateral teeth (d) of the radula, and clausilium plate (e). Scale bars represent 1mm (a–b, e), 50 (c), and 20  $\mu$ m (d).

7e). Such hooks, all with similar positioning, have already been reported from a few, apparently not close-related species of the Phaedusinae. They were found in *Phaedusa bocki* (Sykes, 1895), *P. paviei* (Morlet, 1892), *Loosjesia cambojensis* (Pfeiffer, 1861), *Tyrannophaedusa nankaidoensis* Kuroda, 1955, and *Acanthophaedusa ookuboi* Nordsieck, 2007 (Pilsbry, 1908; Loosjes, 1848; Minato, 1981; Nordsieck, 2007). The apparent homoplasy of this structure seems indicative of some advantageous function. As all these species occur in regions with heavy seasonal rainfall, it seems conceivable that the hook emerging from the outside of the clausilium can ensure better survival during temporary submergence by trapping an air bubble.

Distinctive features of the genital anatomy are the short male organs and relatively long vagina, as well as the lack of a diverticulum at the pedunculus of the bursa copulatrix (Fig. 7a). The penis is wider than the similarly short epiphallus. The retractor muscle is attached to the epiphallus at about quarter length from the end of its wider proximal part. The vagina is nearly of the same length as those of the penis and the epiphallus. The bursa is not clearly separate from the elongate pedunculus. In the studied specimen these organs harboured a spermatophore (Fig. 7b). The radula (Figs 7c–d) consists of rectilinear rows of teeth (Figs 8c–d). In each row the rhomboidal central tooth has a large main cusp between two shorter, triangular ectocones. The adjacent half rows include nine bicuspid lateral teeth and 12 to 13 serrate marginal ones with increasing numbers of cusps toward the edges.

The systematic position of *O. abstrusa* is ambiguous. Conditionally it is placed in the genus *Oospira*, as defined by Nordsieck (2001, 2002b). This composite taxon comprises a large number of morphologically very diverse species (Nordsieck, 2007), sharing merely strong and distinct palatal plicae (Nordsieck, 2001). It is expected that molecular data will soon provide ground for a solid, phylogeny-based generic classification of the species that are currently classified with *Oospira*.

*Oospira naggsi* Luong & Szekeres, 2014

So far *O. naggsi* was known only from two nearby sites in the Cat Tien National Park in Vietnam, Dong Nai Province (Grego *et al.*, 2014;

Fig. 2). Here a new subspecies of it is described, which was discovered about 180km northeast of these localities, in the Hon Ba Nature Reserve of Khanh Hoa Province (Fig. 2).

*Oospira naggsi parva* subsp. nov.  
(Fig. 6c)

*Differential diagnosis* Compared to the nominotypical subspecies, the shell is much smaller and has coarser sculpture, the plica principalis is shorter, the palatal plicae are less deeply positioned.

*Type material* Holotype: Vietnam, Khanh Hoa Province, Suoi Cat Village, Hon Ba Nature Reserve (12°07'21.5" N 108°58'04.5" E, 1080m), leg. B. Fontaine & O. Gargominy 17.11.2013 (MNHN-IM-2012–27205, dry). Paratypes: Vietnam, Khanh Hoa Province, Suoi Cat Village, road to the Hon Ba Nature Reserve (12°07'12.4" N 108°57'2.7" E, 1400m), leg. B. Fontaine & O. Gargominy 14.11.2013 (MNHN-IM-2012–27202/1 and -27203/1, ethanol-preserved).

*Description* The brown, spindle-shaped shell with concave outline consists of 9½ to 10 whorls. The surface of the moderately emerged whorls is glossy, covered by fine and dense riblets that become more distinct at the neck. The aperture is ovoid, its somewhat flattened light brown margin is uninterrupted. The strong and sharp lamella superior is connected to the less emerged lamella spiralis smoothly, without noticeable junction. The well emerged lamella inferior reaches the aperture close and parallel to the superior, then descends in a nearly straight line before terminating very near to the peristome margin. The lamella subcolumellaris, ending just below the final part of the inferior, is inconspicuous but visible in front view of the aperture. The plica principalis runs from the ventrolateral to somewhat beyond the dorsal side. Laterally there are four or five palatal plicae, of which the uppermost is longest, and the central ones are shortest. Of the clausilium plate only its parietal edge is barely visible through the aperture.

*Measurements* Holotype: shell height ( $H_s$ ) 20.7mm, shell width ( $W_s$ ) 4.7mm, aperture height ( $H_a$ ) 4.9mm, aperture width ( $W_a$ ) 3.5mm. Paratypes (2, ethanol-preserved):  $H_s$  19.9 and

20.2mm,  $W_s$  4.8 and 5.0mm,  $H_a$  5.1 and 4.9mm,  $W_a$  3.7 and 3.6mm.

*Etymology* The name refers to the diminished size of this subspecies compared to that of the nominotypical subspecies.

*Remarks* The type material was collected in primary, as well as degraded mountain forests of non-limestone environment. The shell features that distinguish the new subspecies from *O. n. naggsi* possibly result from the higher altitude of the localities (1080 and 1400m), compared to those of the nominotypical subspecies (140 and 170m).

*Castanophaedusa* gen. nov.

Type species: *Castanophaedusa fontainei* sp. nov.

*Differential diagnosis* Differs from other genera by the combination of rhomboidal aperture, on the columellar side extended and sharply bent basis, continuous lamellae superior and spiralis, deep and steeply descending lamella inferior, strongly emerged and marginal lamella subcolumellaris, and the ventral palatal plicae that are parallel to the plica principalis.

*Etymology* The new genus is named after the characteristic dark chestnut shell colour of its species.

In addition to *C. fontainei* sp. nov., the new genus also includes the species that was described as *Oospira huberi* by Nguyen (2016).

*Castanophaedusa fontainei* sp. nov.  
(Fig. 6d)

*Differential diagnosis* Distinguishable from *C. huberi* (Thach, 2016) by its larger shell with concave outline, flattened, stronger sculptured whorls, and its straight, rather than spirally descending lamella inferior.

*Type material* Holotype: Khanh Hoa Province, Suoi Cat Village, Hon Ba Nature Reserve (12°06'52.5" N 108°58'54.9" E, 690m) (Fig. 2), leg. B. Fontaine & O. Gargominy 18.11.2013 (MNHN-IM-2012-27207, dry).

*Description* The shell is large, spindle-shaped, dark reddish-brown. The holotype, lacking the protoconch part, consists of  $8\frac{1}{4}$  whorls.

Teleoconch whorls are covered by dense striae, which become stronger and wider-spaced over the last half whorl. The basis is extended and angular at the columellar side, resulting in an angle that makes the aperture rhomboidal. The dark brown peristome is detached, its margin is wide and flat. The strong and sharp lamella superior ends before reaching the peristome margin. Inward it becomes lower and makes a smooth transition into the lamella spiralis. The terminal part of the lamella inferior, barely visible in front view, descends along a straight line and ends at the columella. The strongly emerged lamella subcolumellaris reaches the peristome margin at its columellar corner. The plica principalis starts post-ventrally, above the sinulus, and terminates dorsally. On the ventral side it is joined by six parallel plicae, of which the intermediate ones are shorter than the upper- and lowermost. The clausilium, invisible through the aperture, could not be studied.

*Measurements* Holotype:  $H_s$  (with broken tip) 27.4mm,  $W_s$  6.4mm,  $H_a$  6.2mm,  $W_a$  5.3mm.

*Etymology* The new species is dedicated to Benoit Fontaine who collected, together with *O. Gargominy*, the studied Vietnamese clausiliids.

*Remarks* The holotype was collected among rock outcrops in a degraded forest. Its broken tip apparently resulted from mechanical injury, rather than decollation. The other species of the genus, *C. huberi*, also occurs in Khanh Hoa Province, near the Yang Bay Waterfalls (Nguyen, 2016), only about 10km north-northeast of the type locality of *C. fontainei* sp. nov. (Fig. 2).

*Castanophaedusa huberi* (Thach, 2016)  
(Fig. 6e)

The superficial original description of this species (Nguyen, 2016) necessitates its redescription. It is based on two specimens from Vietnam, Khanh Hoa Province, Khanh Vinh District, around the Yang Bay Waterfalls (12°11'18" N 108°54'38" E), leg. F. Huber, originating from the same batch as the holotype (NBC 5004194).

*Description* The medium-size, tumid, very dark reddish-brown shell has convex outline. Its  $8\frac{1}{2}$  to 7 strongly bulging whorls are almost smooth, except the last one that is densely striate. The

pointed apex is compressed, its initial whorls widen very rapidly. The basis is extended and angular at the end of the columella. The dark chestnut peristome is rhomboidal, detached, weakly doubled, its margin is wide and flat. The well emerged lamella superior becomes low at its straight transition into the spiralis. The lamella inferior is weakly emerged but well visible in front view of the aperture. It descends in a steep spiral, which becomes hidden behind the columella at half height of the aperture. The strong lamella subcolumellaris ends marginally at the columellar corner of the peristome. The plica principalis initiates post-ventrally, above the sinus, and terminates dorsally. It is joined ventrally by six to seven parallel plicae, of which the intermediate ones are shorter. The clausilium could not be examined.

The above description is based on two specimens originating from the same lot as the type material. Their dimensions are:  $H_s$  19.6 and 19.9mm,  $W_s$  5.8 and 5.9mm,  $H_a$  5.3 and 5.5mm,  $W_a$  4.8 and 4.9mm.

In the original description, published in a book authored by Nguyen Ngoc Thach, the name of this taxon is introduced as "*Oospira huberi* Thach" (Nguyen, 2016, p. 57). Here we follow this usage, but point out that Thach is the author's given name, whereas his family name is Nguyen. Thus, as for all other authors, his publication is cited with the family name.

### *Messageiriella* gen. nov.

Type species: *Messageiriella gargominyi* sp. nov.

*Differential diagnosis* The diagnostic characters of the new genus are those of the type species.

*Etymology* The new genus is named after Martin Messenger in recognition of his great contribution to the uniquely thorough early research of the Vietnamese malacofauna.

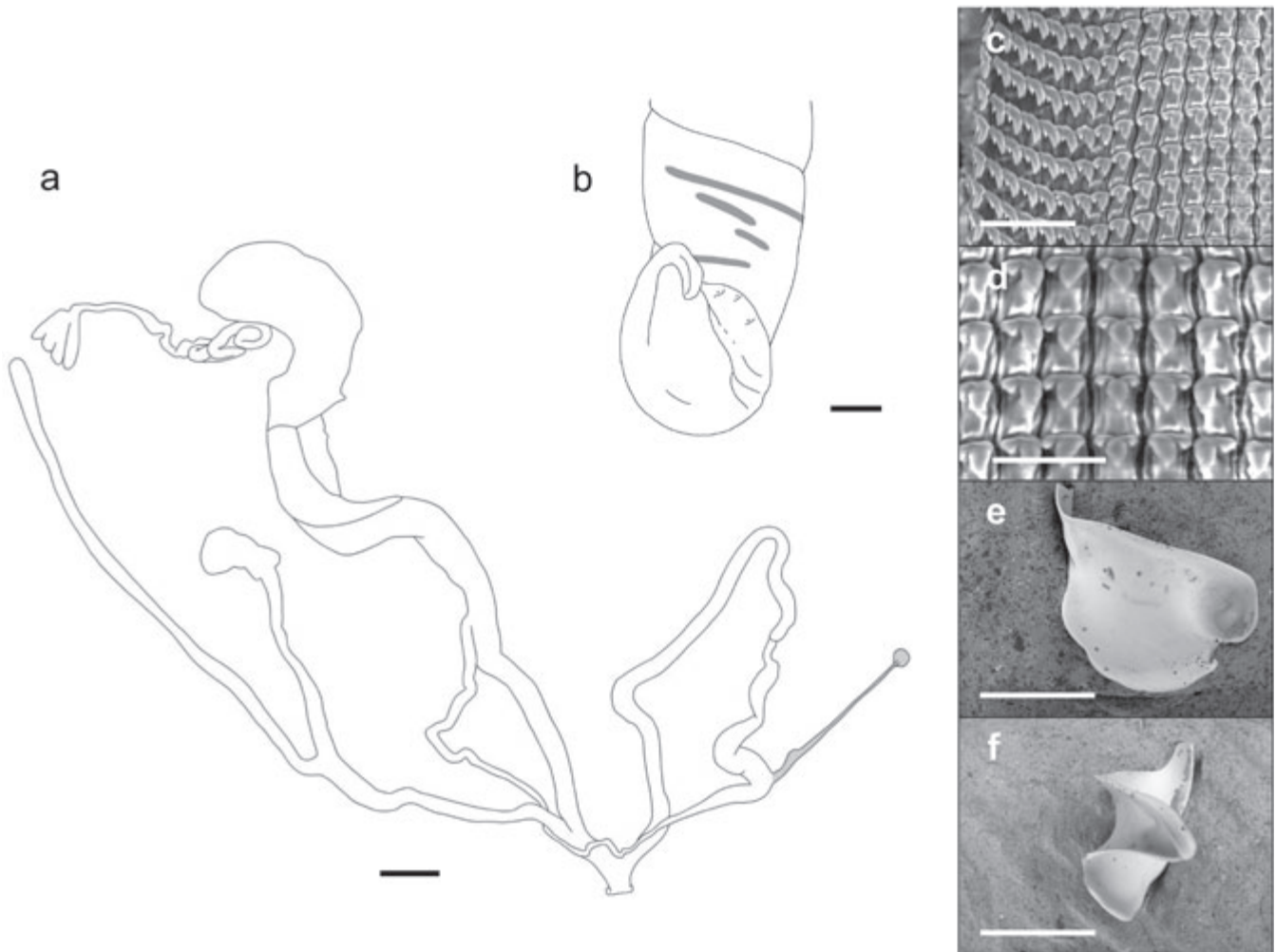
*Messageiriella gargominyi* sp. nov.  
(Figs 6f, 8a–f)

*Differential diagnosis* Medium-size species distinguishable from all other clausiliids of Southeast Asia by the combination of detached aperture, intralamellar plicae, marginally ending lamellae inferior and subcolumellaris, and non-parallel ventral palatal plicae.

*Type material* Holotype: Vietnam, Khanh Hoa Province, Suoi Cat Village, Hon Ba Nature Reserve, near the Yersin Chalet (12°07'07.9" N 108°56'49.9" E, 1500m), leg. B. Fontaine & O. Gargominy 24.11.2013 (MNHN-IM-2012–27208, dry). Paratypes (all from Vietnam, Khanh Hoa Province): Suoi Cat Village, Hon Ba Nature Reserve, Hon Ba Summit (12°06'59.3" N 108°56'40.6" E, 1550m), leg. B. Fontaine & O. Gargominy 13.11.2013 (MNHN-IM-2012–27201/1, ethanol-preserved); Suoi Cat Village, Hon Ba Nature Reserve, at the Yersin Chalet (12°07'10.4" N 108°56'52.4" E, 1500m), leg. B. Fontaine & O. Gargominy 14.11.2013 (MNHN-IM-2012–27204/1, ethanol-preserved, dissected); Suoi Cat Village, Hon Ba Nature Reserve, near the Yersin Chalet (12°07'21.5" N 108°57'21.2" E), 1360m., leg. B. Fontaine & O. Gargominy 17.11.2013 (MNHN-IM-2012–27206/1, ethanol-preserved).

*Description* The light yellow, fusiform shell with wide aperture consists of  $9\frac{1}{2}$  to  $10\frac{1}{2}$  bulging whorls. The surface of the shell is very smooth and glossy, only the last whorl becomes increasingly striate from its dorsal part toward the neck. The basis is rounded. The ovoid, white aperture is detached, its margin is reflexed. The lamella superior is moderately strong, inward it makes a straight and smooth transition into the lamella spiralis. The end part of the lamella inferior is well visible in front view of the aperture. It descends steeply in a straight line before turning around the peristome and reaching its margin. Between the lamellae superior and inferior there are three to five wrinkle-like plicae of varying strength. Right below and parallel to the lamella inferior ends the also marginal lamella subcolumellaris. The plica principalis starts post-ventrally, above the sinus, and terminates dorsolaterally. Under it there are three strong ventral palatal plicae of nearly equal lengths (Fig. 8b). The upper plica slightly diverges from the principalis, but is parallel to the middle one that is less deeply situated. The lower plica starts at the same depth as the upper and converges to the principalis and the two other plicae. The broad calusilium plate is widest near its incised, two-lobed end part (Figs 8e–f).

The genital organs are shown in Fig. 8a. The penis is very long, its border with the somewhat shorter and wider epiphallus is well recognizable. The bursa copulatrix is inflated, its



**Figure 8** *Messengeriella gargominyi* sp. nov.: genital organs (a), plicae (b), central to marginal (c) and central to first two lateral (d) teeth of the radula, and clausilium plate (e–f). Scale bars represent 1mm (a–b, e–f), 50 (c), and 30  $\mu$ m (d).

pedunculus consists of a shorter proximal and a longer distal part. The diverticulum is about twice longer than the proximal pedunculus with the bursa. The radula (Figs 8c–d) has rectilinear rows of teeth. In a row the central tooth is triangular and tricuspid, with large rhomboidal central cusp and small, triangular ectocones. In each half row there are seven bicuspid lateral, and at least six tricuspid marginal teeth.

**Measurements** Holotype:  $H_s$  15.7mm,  $W_s$  4.1mm,  $H_a$  4.0mm,  $W_a$  3.1mm. Paratypes:  $H_s$  17.1mm,  $W_s$  4.7mm,  $H_a$  4.5mm,  $W_a$  3.3mm (Hon Ba Summit);  $H_s$  18.1 and 17.6mm,  $W_s$  4.3 and 4.2mm,  $H_a$  3.9 and 3.6mm,  $W_a$  2.8 and 2.7mm (Yersin Chalet).

**Etymology** The new species is dedicated to Olivier Gargominy who collected, together with B. Fontaine, the studied Vietnamese clausiliids.

**Remarks** With its serrate interlamellar peristome margin, strong ventral plicae, deep positioned and lobed clausilium plate *Messengeriella gargominyi* sp. nov. resembles some species of *Luchuphaedusa* Pilsbry, 1901, a genus known from the Ryukyu Islands of Japan. However, it clearly differs from those by the steeply descending and low ending lamella inferior and, anatomically, by the diverticulum that exceeds the combined lengths of the bursa and proximal pedunculus (Fig. 8a; Minato, 1994). The type material was collected in primary forest areas with rock outcrops.

#### ADDITIONAL SPECIES FROM LAOS

The material collected in Luang Prabang Province contains two further species of the subfamily Phaedusinae that are represented in some

of the samples only by single, poorly preserved specimens.

Fragments of a *Margaritiphaedusa* Nordsieck, 2001 species were collected at the following sites (Fig. 1): 17km SE of Muang Xiang Ngeun, left side of the Nam Khan River (19°41'12.1" N 102°19'11.8" E, 390m), leg. A. Abdou & I. V. Muratov 30.10.2006 (MNHN-IM-2012-27186, perforated body whorl), found together with *Garnieria* (*G.*) *mouhoti*; 17km SE of Muang Xiang Ngeun, left side of the Nam Khan River, 2km S along a small stream (19°40'11.3" N 102°18'32.3" E, 530m), leg. A. Abdou & I. V. Muratov 31.10.2006 (MNHN-IM-2012-27187, apical fragment); immediately NE of Phou Khoun (19°26'47.0" N 102°26'17.4" E, 1180m), leg. A. Abdou & I. V. Muratov 15.11.2006 (MNHN-IM-2012-27189, apical fragment); Mt. Phou Xuang, 1.5km NE of Ban Lak Sip, 5km SE of Luang Prabang (19°51'36.3" N 102°11'04.9" E, 640m), leg. A. Abdou & I. V. Muratov 24.11.2006 (MNHN-IM-2012-27191, apical fragment), found together with *Garnieria* (*G.*) *mouhoti* and *Phaedusa micropaviei*.

A body whorl fragment of a *Phaedusa micropaviei* was collected at Mt. Phou Xuang, 1.5km NE of Ban Lak Sip, 5km SE of Luang Prabang (19°51'36.3" N 102°11'04.9" E, 640m), leg. A. Abdou & I. V. Muratov 24.11.2006 (MNHN-IM-2012-27192). It was found together with *Garnieria* (*G.*) *mouhoti* and *Margaritiphaedusa* sp.

#### ZOOGEOGRAPHICAL CONSIDERATIONS

In contrast to the multitude of Clausiliidae data from the northeastern provinces of Vietnam, records have been very limited from the southern part of this country, and also from Laos. But some recent results (Nordsieck, 2002a, 2003; Grego *et al.*, 2014; Nguyen, 2016) and our present data already give a sketchy picture of the abundance and diversity of this snail family in the aforementioned regions of Indochina.

One characteristic aspect is the sporadic and scarce occurrence of relatively few clausiliid species. This, even if partly attributable to limited exploration of the area, seems to indicate geomorphological and climatic conditions that are mostly unfavourable for these snails. Compared to the conditions of northeastern Vietnam, their dispersal and survival is likely limited by the dry seasons that are longer and more severe, as well as the smaller and more sporadic forestlands

confined mostly to high altitudes in non-limestone regions. Fig. 1 shows that of 98 samples collected in Laos only 14 contained clausiliids, and 11 of these only a single species.

Another intriguing zoogeographical aspect is that the few clausiliid species known from the southern Dong Nai, Khanh Hoa and Lam Dong Provinces of Vietnam show little morphological similarity to those of other regions in Indochina. The two endemic genera and the *Oospira* taxa resembling congeneric species in Indonesia (Grego *et al.*, 2014) suggest that the elements of this fauna evolved independently from those of northern Vietnam and Laos. Identifying their origins will certainly be a fascinating challenge for future molecular phylogenetic studies.

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