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Systematics of the family Plectopylidae in Vietnam with additional information on Chinese taxa (Gastropoda, Pulmonata, Stylommatophora)

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Abstract

Vietnamese species from the family Plectopylidae are revised based on the type specimens of all known taxa, more than 600 historical non-type museum lots, and almost 200 newly-collected samples. Altogether more than 7000 specimens were investigated. The revision has revealed that species diversity of the Vietnamese Plectopylidae was previously overestimated. Overall, thirteen species names (*anterides* Gude, 1909, *bavayi* Gude, 1901, *congesta* Gude, 1898, *fallax* Gude, 1909, *gouldingi* Gude, 1909, *hirsuta* Möllendorff, 1901, *jovia* Mabille, 1887, *moellendorffi* Gude, 1901, *persimilis* Gude, 1901, *pilsbryana* Gude, 1901, *soror* Gude, 1908, *tenuis* Gude, 1901, *verecunda* Gude, 1909) were synonymised with other species. In addition to these, *Gudeodiscus hemmeni* **sp. n.** and *G. messageri raheemi* **ssp. n.** are described from north-western Vietnam. Sixteen species and two subspecies are recognized from Vietnam. The reproductive anatomy of eight taxa is described. Based on anatomical information, *Halongella* **gen. n.** is erected to include *Plectopylis schlumbergeri* and *P. fruhstorferi*. Additionally, the genus *Gudeodiscus* is subdivided into two subgenera (*Gudeodiscus* and *Veludiscus* **subgen. n.**) on the basis of the morphology of the reproductive anatomy and the radula. The Chinese *G. phlyarius werneri* Páll-Gergely, 2013 is moved to synonymy of *G. phlyarius*. A spermatophore was found in the organ situated next to the gametolytic sac in one specimen. This suggests that this organ in the Plectopylidae is a diverticulum. Statistically significant evidence is presented for the presence of calcareous hook-like granules inside the penis being associated with the absence of embryos in the uterus in four genera. This suggests that these probably play a role in mating periods before disappearing when embryos develop. *Sicradiscus mansuyi* is reported from China for the first time.

Keywords
Anatomy, revision, taxonomy, new species, Plectopylidae, Corillidae, mating behaviour, Vietnam, China

Introduction

At present, 477 species and subspecies in 22 families of terrestrial pulmonates are known from Vietnam (Schileyko 2011). As in other southeast Asian gastropods, most of these (77%) were described between 1880 and 1920 with poor locality data and based on shell characters only. Several species were described by examining only a single shell. Internal anatomy and exact collecting locality have been documented only for a few taxa. Accordingly, the systematics of most Vietnamese land snails remains questionable. Without accurate knowledge on their distribution and taxonomy, the recognition of possible threats and the subsequent establishment of appropriate conservation measures of these populations are impossible.

The Plectopylidae are currently the fifth largest pulmonate family in Vietnam with 28 species, after the Camaenidae s.l. (=Camaenidae and Bradybaenidae: 127 sp., 9 ssp.), Clausiliidae (84 sp., 10 ssp.), Ariophantidae (68 sp., 3 ssp.) and Streptaxidae (47 sp., 2 ssp.) (Schileyko 2011). The Plectopylidae are a group of medium sized (5–35 mm), usually flat, sinistral or dextral species, which have internal lamellae and plicae on both the palatal and parietal walls. This family is currently included within the Plectopyloidea together with the south Asian family Corillidae Pilsbry, 1905 and the south-west family African Sculptariidae Degner, 1923 (Bouchet and Rocroi 2005). However, Schileyko (1999) classified Sculptariidae in the superfamily Acavoidea. Plectopylidae differ from the probably closest group, which are the Corillidae with one or two vertical lamellae on the parietal wall. The mainly Sri Lankan Corillidae only have horizontal plicae. Plectopylidae have a wide distribution from northeastern India through the majority of southeast Asia to Peninsular Malaysia, northern Vietnam and southern Japan (Páll-Gergely and Hunyadi 2013 and references therein).

Morlet (*schlumbergeri*; 1886a, 1886b) was the first to describe a Vietnamese plectopylid species. Mabille (*jovia* and *phlyaria*; 1887a, 1887b), Ancey (*villedaryi*; 1888), Fischer (*giardi* and *francoisi*: 1898b, 1898a) and Möllendorff (*choanomphala*, *emigrans*, *fruhstorferi*, *hirsuta*: 1901) followed. Gude (1897b, 1899a, 1899b, 1899c, 1899d, 1900, 1901a, 1901b, 1901c, 1908, 1909) described new species, revised the taxa and published drawings of every species that had not been previously figured. He received most of the shell material from French collectors, mainly from Messager and Mansuy.

Gude (1899c) proposed the subgeneric division of *Plectopylis* (equivalent to the current Plectopylidae) by erecting seven "sections" (subgenera) within *Plectopylis*: *Endothyra* (replaced by *Endothyrella* by Zilch 1960), *Chersaecia*, *Endoplon*, *Plectopylis*, *Sinicola*, *Enteroplax* and *Sykesia* Gude, 1897a. The last two have been removed from the Plectopylidae; *Enteroplax* has been placed in the Strobilopsidae (Zilch 1959; Solem 1968; Schileyko 1998). Gude (1914) and Schileyko (2001) assigned *Ruthvenia* Gude, 1911 (nomen novum pro *Sykesia*) to the Endodontidae and Schileyko (2010) and Raheem et al. (2014) to the Charopidae. Gude's (1899c) subdivision was primarily based on the morphology of palatal plicae, the direction of coiling and the depth of the umbilicus.

According to Gude (1899c), only the "section" *Endoplon* Gude, 1899 occurs in Vietnam. Gude also placed two Burmese (Myanmar) species (including the type species, *Helix brachyplecta* Benson, 1863) in *Endoplon*. Some Vietnamese species were subsequently placed in the subgenus *Sinicola* (Möllendorff 1901, Gude 1908). However, in some species descriptions Gude did not specify subgenera (Gude 1901a, 1908, 1909) or these were mentioned only within the text (Gude 1908). He mentioned *Plectopylis tenuis* as the connection between *Sinicola* and *Endoplon* (1908). Schileyko (1999) elevated Gude's (1899c) "sections" (*Endothyrella*, *Chersaecia*, *Endoplon*, *Plectopylis*, *Sinicola*) to genera. Schileyko (1999) followed Yen (1939) and Zilch (1960) in placing the Chinese genus *Amphicoelina* Haas, 1933 within the Plectopylidae but Páll-Gergely & Asami (2014) classified *Amphicoelina* within the Camaenidae, as originally proposed by Haas (1933).

After Gude's publications, virtually no taxonomic information was published on Vietnamese members of the family. Jaeckel (1950) reported two juvenile shells of "*Plectopylis laminifera*" from the debris of an unknown Tonkinese (northern Vietnamese) river. Páll-Gergely and Hunyadi (2013) concluded that juvenile shells of *Sinicola jugatoria* (Ancey, 1885) (synonym: *laminifera*) cannot be distinguished from congeners, that their distribution in China (northern Chongqing, eastern Hubei and Guizhou provinces) lies far from Vietnam, and that it probably does not occur within the country.

Revision of the Chinese Plectopylidae (Páll-Gergely and Hunyadi 2013) also revealed that the two recorded Burmese species of *Endoplon* show considerable differences from Vietnamese species. Vietnamese species have regularly ribbed embryonic whorls and no long horizontal parietal plicae, whereas the Burmese species possess a comparatively smooth protoconch and long horizontal parietal plica. Because the type species of *Endoplon* is one of the Burmese species, all the former Vietnamese *Endoplon* species were moved to a new genus, *Gudeodiscus* Páll-Gergely, 2013. The two Burmese *Endoplon* species are probably closely related to *Plectopylis* and *Chersaecia* species, which inhabit similar geographic regions (Myanmar, northern Thailand and northeastern India) (Páll-Gergely and Hunyadi 2013).

The genus *Sinicola* Gude, 1899 (with the type species *Helix fimbriosa* von Martens, 1875) differs from *Gudeodiscus* mainly in the keeled body whorl (rounded in *Gudeodiscus*) and the presence of deciduous periostracal folds in most species (always absent in *Gudeodiscus*). Former Vietnamese *Sinicola* species (*emigrans*, *fruhstorferi*, *soror* and *suprafilaris*) were all classified within *Gudeodiscus* by Páll-Gergely and Hunyadi (2013). So far, *Sinicola* species have only been found to inhabit Chinese provinces (Chongqing, northern Guangxi, Guizhou, Hubei, Hunan and Sichuan). The third genus, *Sicradiscus* Páll-Gergely, 2013 (Type species. *Plectopylis schistoptychia* Möllendorff, 1886) was established for some small bodied species. *Sicradiscus* consists of two species groups. One has a rounded body whorl and a strong apertural fold: *S. invius* (Heude, 1885), *feheri* Páll-Gergely & Hunyadi, 2013, *S. mansuyi* (Gude, 1908) (only Vietnamese species of the genus) and *S. securus* (Heude, 1885). The other species group possesses a moderately shouldered body whorl and lacks an apertural fold: *S. cutisculptus* (Möllendorff, 1882), *S. diptychia* (Möllendorff, 1885), *S. hirasei* (Pilsbry, 1904), *S. ishizakii* (Kuroda, 1941) and *S. schistoptychia*. *Sicradiscus transitus* Páll-Gergely, 2013 with an apertural fold and a shouldered body whorl connects these two species groups. All *Sicradiscus* species differ from *Sinicola* by the presence of the anterior lamella. The rounded *Sicradiscus* differs from *Gudeodiscus* by the small size, strong apertural fold connected to the callus and the smooth ventral surface.

For the present revision of the Vietnamese Plectopylidae, we examined all the type specimens as well as many available non-type material deposited in public institutions. All samples deposited in HNHM, NHMSB, NHM, MNHN, NHMW, SMF and SNM were investigated. Some "problematic" samples were loaned and identified from RBINS and USNM. Material (usually with GPS data) obtained from the following private collections were investigated: András Hunyadi, Jozef Grego, Christa and Jens Hemmen, Kenji Ohara, Jamen Uiriamu Otani and Wim Maassen. Altogether approximately two hundred samples with exact locality data were examined. Fischer and Dautzenberg (1904) mentioned two names (*Plectopylis anoplon* and *simulans*) from Vietnam but presented no formal descriptions. Although listed by Thanh (2008), these nomen nuda cannot be assigned to species. Gude's material is deposited in NHM, and most samples from Lieutenant Colonel Messager are housed in MNHN. Messager probably sent only a few shells to Gude, who published on these in 1909. The six species described by Gude (1909) are problematic. Investigation of these specimens including Messager's original material allowed us to gain a better understanding of species boundaries based on morphological gaps in continuously varying shell characters.

Here we present the outcome of systematic revision of Vietnamese Plectopylidae (see summary in Table 1) with reproductive anatomy and radula morphology of eight species. Additionally, we publish information on the radula of fifteen Chinese species. The genus *Gudeodiscus* is divided into two subgenera based on anatomical and radula information of Chinese and Vietnamese species.

Materials and methods

Shell whorls (exactness 0.25) were counted according to Kerney and Cameron (1979: 13). Differences in size are indicated in the diagnosis using the following terms: very small (6–10 mm), small (10–15 mm), medium-sized (15–20 mm), large (20–25 mm), very large (25–30 mm).

The palatal plicae can be observed from the interior and exterior view. This is indicated in the figure captions in all cases. If enough shell material was available, a shell fragment with the palatal plicae was broken out and the lamellae were observed directly (interior view). If shell material was limited, the plicae are figured as they were

Table 1. (Sub)generic division of Vietnamese Plectopylidae in Gude's (1899c) revision, in the original description (in case of species described after Gude 1899c), and in this study. Synonymies are also indicated. Valid taxa with ***bold italic***.

(sub)species	section in Gude 1899c	(sub)genus in the original publication	This study	synonym of
anceyi Gude, 1901		not specified	*Gudeodiscus* (*Gudeodiscus*?)	
anterides Gude, 1909		not specified		*phlyarius*
bavayi Gude, 1901		not specified		*francoisi*
choanomphala Möllendorff, 1901		*Endoplon*		*villedaryi*
congesta Gude, 1899	*Endoplon*			*giardi*
cyrtochila Gude, 1909		not specified	*Gudeodiscus* (*Gudeodiscus*?)	
dautzenbergi Gude, 1901		not specified	*Gudeodiscus* (*Gudeodiscus*)	
emigrans Möllendorff, 1901		*Sinicola*	*Gudeodiscus* (*Veludiscus*)	
fallax Gude, 1909		not specified		*phlyarius*
fischeri Gude, 1901		not specified	*Gudeodiscus* (*Gudeodiscus*)	
francoisi Fischer, 1898	*Endoplon*		*Gudeodiscus* (*Gudeodiscus*?)	
fruhstorferi Möllendorff, 1901		*Sinicola*	*Halongella*	
giardi Fischer, 1898	*Endoplon*		*Gudeodiscus* (*Gudeodiscus*)	
gouldingi Gude, 1909		not specified		*phlyarius*
hirsuta Möllendorff, 1901		*Endoplon*		*schlumbergeri*
infralevis Gude, 1908		not specified	*Gudeodiscus* (*Gudeodiscus*?)	
jovia Mabille, 1887	*Endoplon*			*schlumbergeri*
lepida Gude, 1900		not specified		*francoisi*
mansuyi Gude, 1908		not specified	*Sicradiscus*	
messageri Gude, 1909		not specified	*Gudeodiscus* (*Gudeodiscus*)	
moellendorffi Gude, 1901	*Endoplon*			*phlyarius*
persimilis Gude, 1901		not specified		*dautzenbergi*
phlyarius Mabille, 1887	*Endoplon*		*Gudeodiscus* (*Gudeodiscus*)	
pilsbryana Gude, 1901 (new name for *villedaryi*)		not specified		*schlumbergeri*
quadrilamellatus Páll-Gergely, 2013		*Gudeodiscus*	*Gudeodiscus* (*Veludiscus*)	
schlumbergeri Morlet, 1886	*Endoplon*		*Halongella*	
soror Gude, 1908		*Sinicola*		*infralevis*
suprafilaris Gude, 1908		*Sinicola*	*Gudeodiscus* (*Gudeodiscus*?)	
tenuis Gude, 1901		not specified		*fischeri*
verecunda Gude, 1909		not specified		*phlyarius*
villedaryi Ancey, 1888	*Endoplon*		*Gudeodiscus* (*Gudeodiscus*)	

visible through the shell wall (external view). For nomenclature of lamellae (vertical parietal folds) and plicae (horizontal parietal folds and palatal folds) see Figure 1.

Examined specimens for each taxon are separately listed as types, museum material and new material. Most specimens in the last category are geo-referenced whereas precise localities are unknown for the majority of older museum material. The original code of locality is indicated before the locality of newly collected material. Certain populations are referred to by using these codes, and the inventory numbers in case of museum material, for example in the measurements and species remarks. In the distri-

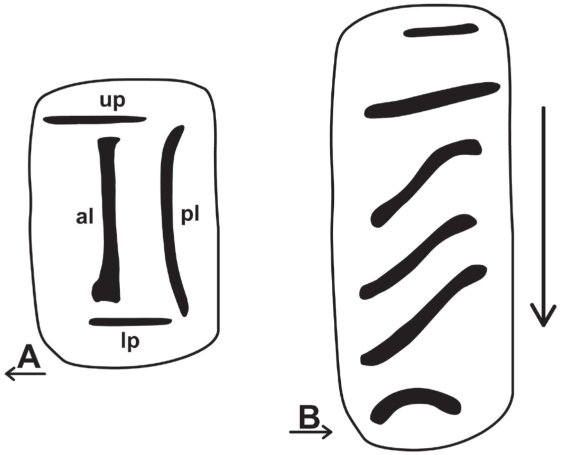

Figure 1. Nomenclature of parietal (**A**) and palatal (**B**) plicae and lamellae. Small arrows under the letters show the direction of the aperture. Large arrow next to figure B shows the direction of counting of palatal plicae (first above, last below). Abbreviations: al: anterior lamella; lp: lower plica; pl: posterior lamella; up: upper plica.

Table 2. Co-occurrence of Vietnamese Plectopylidae. Three stars indicate co-occurrence observed with newly-collected materials, which were collected by the same collector in each strict sympatry. Two stars indicate that the two species were collected at geographically close sites by the same or different collectors (*anceyi-fischeri*: 940 m; *dautzenbergi*-cf. *phlyarius*: 1160 m; *anceyi-suprafilaris*: 2340 m; *fischeri-emigrans quadrilamellatus*: 4650 m; *francoisi-phlyarius*: 85 m; *francoisi-suprafilaris*: 290 m; *giardi-phlyarius*: 350 m; *phlyarius-suprafilaris*: 370 m; *phlyarius-mansuyi*: 350 m). One star indicates frequent presence of the two species mixed within museum samples.

	anceyi	***fischeri***	***francoisi***	***giardi***	***phlyarius* (*gouldingi/ fallax*)**	***phlyarius***	***hemmeni* sp. n.**	***mansuyi***
cyrtochilus								***
dautzenbergi						**		
fischeri	**							
francoisi	***							
giardi	***		***					***
messageri					*			
***messageri raheemi* ssp. n.**						***	***	
phlyarius	***		**	**				**
emigrans quadrilamellatus	***	**						
suprafilaris	**		**	***		**		***
villedaryi	***					***		

bution maps, localities which are closer to each other than 2 km were indicated with a single plot to make the map easier to understand. Chinese localities published by Páll-Gergely and Hunyadi (2013) are also indicated on the maps. The distances between parapatric populations (Table 2) were measured using Google Earth.

Table 3. Association between the presence of calcareous granules in the penis and embryos in the uterus in the genera of "Eastern Plectopylidae". Source of information: 1: this study, 2: Páll-Gergely and Hunyadi (2013), 3: Páll-Gergely and Asami (2014).

Name	source	Country, province	elevation (m)	date	embryos	shape of granules	No. of specimens	Notes
G. emigrans otanii	3	China, Guangxi	180	November 13	present	no granules	2	the third specimen was aphallic
G. eroessi eroessi	3	China, Guangxi	153	November 9	present	no granules	2	
G. fischeri	1	Vietnam, Tuyên Quang	70	March 19	absent	hook-like	1	
G. fischeri	1	Vietnam, Bắc Kạn	335	November 19	present	no granules	1	
G. giardi giardi	1	Vietnam, Cao Bằng	430	November 16	absent	hook-like	1	
G. giardi giardi	3	China, Guangxi	308	January 10	absent	flat, oval	1	
G. messageri raheemi	1	Vietnam, Hòa Bình	1120	October 15	present	no granules	1	
G. multispira	2	China, Guangxi	160	October 14	present	no granules	3	
G. multispira	3	China, Guangxi	252	November 12	present	no granules	1	
G. okuboi, specimen1	3	China, Guangxi	131	November 9	present	no granules	1	
G. okuboi, specimen2	3	China, Guangxi	131	November 9	absent	no granules	1	
G. phlyarius	1	Vietnam, Lạng Sơn	370	April 1	present	no granules	1	
G. phlyarius	2	China, Guangxi	190	October 11	absent	hook-like	1	
G. phlyarius	2	China, Guangxi	360	October 23	present	no granules	1	
G. phlyarius ("*fallax*")	1	Vietnam, Lào Cai	270	October 4	absent	flat, oval	2	
G. pulvinaris pulvinaris	3	Hong Kong	300-500	June	absent	hook-like	1	
G. pulvinaris robustus	2	China, Guangxi	140	October 17	present	no granules	1	
G. villedaryi	1	Vietnam, Thái Nguyên	365	May 20	present	no granules	1	
G. villedaryi	1	Vietnam, Thái Nguyên	365	November 12	absent	hook-like	1	
H. fruhstorferi	1	Vietnam, Quảng Ninh	20	August 14	present	very thin, flat, no particular shape	1	
H. schlumbergeri	1	Vietnam, Hải Phòng	20	April 4	present	flat, thin, with no particular shape	1	
Sch. schlumbergeri	1	Vietnam, Hải Phòng	30	November 22	absent	flat, thin, with no particular shape, or T-shaped	1	
Sic. invius	3	China, Sichuan	1087	September 17	absent	no granules	2	

Sic. mansuyi	1	Vietnam, Cao Bằng	570	May 28	present	no granules	2	subadult
Sic. schistoptychia	2,3	China, Hunan	450	November 11	present	tiny flat rounded granules	1	
Sic. transitus	3	China, Guangxi	650	September 12	absent	minute, flat, rounded	1	subadult
Sin. asamiana	3	China, Sichuan	860	September 16	present	no granules	1	
Sin. emoriens	2,3	China, Guangxi	125	November 8	present	no granules	2	
Sin. fimbriosa	2	China, Hunan	590	October 20	absent	no granules	1	subadult
Sin. murata	3	China, Sichuan	860	September 16	present	no granules	1	
Sin. murata	3	China, Sichuan	1090	September 17	present	no granules	1	
Sin. reserata azona	3	China, Guizhou	863	May 10	present	no granules	1	
Sin. stenochila	3	China, Hubei	220	November 3	absent	globular or elongated	2	

Table 4. Association of the presence of embryo and the absence of granules within the genus *Gudeodiscus*.

		embryo		**Probability**
		present	**absent**	
granule	**present**	0	7	0.0001
	absent	12	1	

Table 5. Association of the presence of embryo and the absence of granules within all four genera (*Gudeodiscus*, *Halongella* gen. n., *Sicradiscus*, *Sinicola*).

		embryo		**Probability**
		present	**absent**	
granule	**present**	3	10	0.0006
	absent	18	3	

Ethanol-preserved specimens were dissected under a Leica stereomicroscope, with camera attached to provide photographs of the genital structure from which drawings were produced. In description of the reproductive system, we used the terms "distal" and "proximal" in relation to the genital atrium. At dissection of each specimen, we recorded whether embryos are present in the uterus and calcareous granules on the internal surface of penis (Table 3). Fisher's exact test was used to examine the association of the presence of embryo and the absence of granules by treating all the examined individuals as replicates across the four genera because of limited sample sizes in each genus (Tables 4–5).

To demonstrate the continuous variation of shell heights and diameters across *Plectopylis anterides*/*gouldingi*, *P. fallax*, and *P. fallax* var. *major* specimens (synonyms of *Gudeodiscus phlyarius*; Figure 16), we randomly selected a few samples which can be assigned to those taxa.

The buccal mass was removed and soaked in 2 molar KOH solution for 5 hours before extracting the radula, which was preserved in 70% ethanol. Radulae were directly observed without coating under a low vacuum SEM (Miniscope TM-1000, Hitachi High-Technologies, Tokyo).

Taxonomic treatment

This revision is based on morphology by examination of specimens and literature. Thus the present taxa are defined based on their morphological differences. The present species are hypothesized as species defined by the biological species concept (Mayr 1942), although evidence for differences in sympatry was not always available within the relevant species group. Table 2 shows sympatric species pairs. No specimens were found that show transitional characters between sympatric species. This suggests that these are biological species reproductively isolated from each other.

Previously recognized taxa are synonymized when their differences between traditionally recognized species (often present as only a few individuals) are considered to be very minor. Sometimes, these differences (mainly in the morphology of the plicae and lamellae) show a geographical pattern. If these minor differences fall within the range of the species' morphological diversity, the taxa are synonymized.

Abbreviations

HA Collection András Hunyadi (Budapest, Hungary);
HE Collection Hemmen (Wiesbaden, Germany);
HNHM Magyar Természettudományi Múzeum (Budapest, Hungary);
JG Collection Jozef Grego (Banská Bystrica, Slovakia);
NHMSB Natural History Museum, Sibiu (Romania), Bielz collection;
NHM & **NHMUK** Natural History Museum, London;
MNHN Muséum National d'Histoire Naturelle (Paris, France);
NHMW Naturhistorisches Museum Wien (Vienna, Austria);
OK Collection Kenji Ohara, Nishinomiya Shell Museum (Nishinomiya, Japan);
PGB Collection Barna Páll-Gergely (Mosonmagyaróvár, Hungary);
RBINS Royal Belgian Institute of Natural Sciences (Brussels, Belgium);
SMF Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Germany);
USNM Smithsonian National Museum of Natural History (Washington, USA);
VA Collection András Varga (Gyöngyöshalász, Hungary);
WM Collection Wim J. M. Maassen (Echt, The Netherlands);
ZMUC Zoological Museum, University of Copenhagen (Denmark);
coll collection of
jb juvenile/broken shells

leg collected by
ex from the collection of
D shell diameter
H shell height

Results

Radula information

Information on the radula morphology of Chinese Plectopylidae species has never been published. To provide a comprehensive basis of the radula morphology of Vietnamese species, we publish images of the radula of some Chinese species as well. The key characters of the radula (size of the central tooth in relation to the ectocone of the first lateral, the shape of the mesocone of the first lateral and the morphology of the marginals) are compiled in Table 6.

The overall morphology of the radula was similar in all species. The lateral teeth are arranged along straight rows, whereas the marginals stand in oblique rows. The distinction between the last laterals and the first marginals is not easy, especially in those specimens in which their morphology (bi- or tricuspid) does not differ. Therefore, the data on the number of laterals and marginals are only guidelines.

Systematic treatment

Family Plectopylidae Möllendorff, 1898

Genus *Gudeodiscus* Páll-Gergely, 2013

2013 *Gudeodiscus* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 4, 8.

Type species. *Plectopylis phlyaria* Mabille, 1887, by original designation.

Included taxa. Subgenus *Gudeodiscus* and subgenus *Veludiscus* subgen. n.

Diagnosis. Shell rarely small, usually middle sized or large, dextral, body whorl rounded, without periostracal folds on the "upper keel" of the whorls. The whole protoconch is usually very finely, regularly ribbed (see Figure 10A). The only known exceptions are *Gudeodiscus villedaryi* (see Figure 10B) and *G. dautzenbergi*. Teleoconch usually has a reticulated sculpture; more prominent on the dorsal side; sometimes with very small periostracal filaments, but these are always arranged radially, never in spiral lines. A short apertural fold is present in the majority of the species. Palatal plicae usually 6, sometimes 5 or 7, they are usually free, very rarely connected by a ridge. Middle palatal plicae can be horizontal, oblique or almost vertical, they are usually depressed

Table 6. Key characters of the radula of Chinese and Vietnamese Plectopylidae species. Abbreviations: **L** lateral **M** marginal.

taxon	L	M	size of central	shape of the first lateral	morphology of the marginals
G. (V.) emigrans otanii	9	11	slightly smaller than the ectocone of the first lateral	rhomboid, rather blunt	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
G. (V.) eroessi	10	10	smaller than the ectocone of the first lateral	rhomboid, rather blunt	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
G. (V.) okuboi	7	13	slightly smaller than the ectocone of the first lateral	rhomboid, rather blunt	tricuspid with blunt inner cusp and shallow incision between the inner two cusps
G. (V.) pulvinaris pulvinaris	7	14	smaller than the ectocone of the first lateral	rhomboid, rather blunt	tricuspid with blunt inner cusp and shallow incision between the inner two cusps
G. (G.) fischeri	9	13	as large as or larger than the ectocone of the first lateral	rhomboid, pointed	tricuspid, inner two rather blunt, incision between them deep
G. (G.) giardi	12	15	as large as the ectocone of the first lateral	rhomboid, pointed	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
G. (G.) messageri raheemi	8	16	as large as or larger than the ectocone of the first lateral	rhomboid, pointed	tricuspid with rather sharp inner cusp and deep incision between the cusps
G. (G.) multispira	9	14	as large as or larger than the ectocone of the first lateral	slender oval	tricuspid with rather blunt inner cusp and deep incision between the cusps
G. (G.) phlyarius	9	12	as large as the ectocone of the first lateral	rhomboid, pointed	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
G. (G.) villedaryi	9	10	as large as or slightly smaller than the ectocone of the first lateral	rhomboid, pointed	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
H. fruhstorferi	8	12	much smaller than the ectocone of the first lateral	slender rhomboid	mostly bicuspid, some of them tricuspid with blunt inner cusps
H. schlumbergeri	10	14	smaller than the ectocone of the first lateral	oval	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
Sic. invius	7	8	as large as or larger than the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them
Sic. mansuyi	8	10	as large as the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them, some of them quadricuspid
Sic. schistoptychia	6	14	as large as or larger than the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them

taxon	L	M	size of central	shape of the first lateral	morphology of the marginals
Sic. transitus	6	10	as large as the ectocone of the first lateral	triangular	tricuspid with pointed cusps and deep incision between them
Sin. asamiana	8	11	as large or almost as large as the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them
Sin. emoriens	6	14	as large as or larger than the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them
Sin. fimbriosa	10	15	larger than the ectocone of the first lateral	slender with concave inner line	tricuspid with pointed cusps and deep incision between them
Sin. jugatoria	9	12	as large as the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them
Sin. murata	8	12	as large as the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them
Sin. reserata azona	11	14	as large as the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them
Sin. stenochila	8	13	as large as the ectocone of the first lateral	slender with parallel, straight margins and pointed end	tricuspid with pointed cusps and deep incision between them

"Z" or "V"-shaped. The first plica is always straight and parallel with the suture, the last is slightly curved or oblique. On the parietal wall there are two vertical lamellae or the anterior one is missing or dissolved into small denticles or parallel horizontal plicae. Usually horizontal plicae are visible above and below the anterior lamella, near the sutures.

Penial caecum usually present (very rarely absent). Penis internally with longitudinal folds; the middle or proximal portion of the penis can have transverse or reticulated sculpture; the longitudinal folds are thickened on the apical part of the penis and form "pockets", each of which holds a calcareous, usually hook- or claw-like translucent granule; these granules are probably present seasonally when the snails are reproductively active and disappear when embryos develop in the uterus; the pockets stand in one row or rarely in two rows on the opened penis wall. Epiphallus with simple internal longitudinal folds.

Differential diagnosis. The body whorl of the species belonging to *Sinicola* is keeled or shouldered, often with flat, deciduous periostracal folds arranged in one row on the keel. In contrast, all *Gudeodiscus* species have rounded body whorl and never have periostracal folds arranged in a spiral line. Moreover, in *Sinicola* there are no "pockets" on the inner wall of the penis. The shells of *Halongella* gen. n. are indistinguishable from those of *Gudeodiscus*. *Halongella* gen. n. species have parallel, longitudinal folds on the inner wall of the penis with tiny, flat calcareous granules between the folds, all along the penis; there are no determined "pockets" for the granules at the apical part of the penis, which are so characteristic for *Gudeodiscus*. Additionally, the longitudinal folds inside the epiphallus of *Halongella* gen. n. species have characteristic transverse projections which overlap with those of neighbouring folds. In contrast, *Gudeodiscus* species have parallel folds on the inner wall of the epiphallus. Additionally, most anatomically examined *Gudeodiscus* specimens had a penial caecum, which is missing in both *Halongella* gen. n. species. See also under *Sicradiscus*.

Subgenus *Gudeodiscus* Páll-Gergely, 2013

Diagnosis. Shell indistinguishable from *Gudeodiscus* (*Veludiscus*) subgen. n. Anatomy: The epiphallus has a somewhat thickened proximal part; retractor muscle simple, inserts on the distal end of the penial caecum, or if it is missing, than on the distal end of the penis (at the penis-epiphallus transition). Radula: central tooth usually as large as or slightly larger than the ectocone of the first lateral; mesocone of the first lateral is moderately wide, in most cases has parallel edges. Marginals usually tricuspid with rather pointed inner cusp and rather deep incision between the inner two cusps.

Included taxa. *anceyi* (Gude, 1901)(?), *concavus* Páll-Gergely, 2013(?), *cyrtochilus* (Gude, 1909)(?), *dautzenbergi* (Gude, 1901), *fischeri* (Gude, 1901), *francoisi* (Fischer, 1899)(?), *giardi* (Fischer, 1898), *hemmeni* Páll-Gergely & Hunyadi, sp. n.(?), *infralevis* (Gude, 1908)(?), *marmoreus* Páll-Gergely, 2014(?), *messageri* (Gude, 1909), *multispira*

(Möllendorff, 1883), *phlyarius* (Mabille, 1887), *soosi* Páll-Gergely, 2013(?), *suprafilaris* (Gude, 1908)(?), *ursula* Páll-Gergely & Hunyadi, 2013(?), *villedaryi* (Ancey, 1888), *yanghaoi* Páll-Gergely & Hunyadi, 2013(?), *yunnanensis* Páll-Gergely, 2013(?).

Remarks. All known *Gudeodiscus* species remain in this subgenus with the exception of *G. goliath* Páll-Gergely & Hunyadi, 2013 because of its similar shell and distribution area to *G. pulvinaris robustus* Páll-Gergely & Hunyadi, 2013 and *G. emigrans otanii* Páll-Gergely & Hunyadi, 2013. Those with unknown anatomy and radula morphology have questionable subgeneric assessment. The shell of *G. dautzenbergi* is very similar to the nearby occurring *G. villedaryi*, therefore we think there is no need to question the subgeneric status.

***Gudeodiscus* (*Gudeodiscus*?) *anceyi* (Gude, 1901)**

Figures 2B, 9G, 11C–F

1901a *Plectopylis Anceyi* Gude, Journal de Conchyliologie, 49: 208–209., Figs 6a–e, Plate 6, Figs 6a–c. ["Bac-Kan (le type); secteur de Nac-Ri; entre Cho-Moi et That-Khé"]

2013 *Gudeodiscus anceyi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

Types examined. Tonkin, Bac-Kan, leg. Messager, MNHN 24600 (syntype, Figure 2B); Tonkin, Bac-Khan, NHMW 50858 (2 syntypes).

Museum material examined. Tonkin, coll. Jetschin ex Berlier 1908, SMF 118124/2; Tonkin, Bac-Khan, coll. Jaeckel, S. H. ex Rolle, SMF 207668/1; Tonkin, Bac-Khan, coll. Dosch ex Rolle, SMF 172078/4; Tonkin, Than-Moi, probably ex Messager, SMF 150135/1; Central-Tonkin, Chiam-Hoa, coll. Möllendorff ex Fruhstorfer SMF 150134/1; Tonkin, Bac-Kan, leg. Messager, 22.11.1898, RBINS/5; Secteur de Nac-Ri, RBINS/1; Secteur de Nac-Ri, leg. Messager (n. 33), RBINS/1; Tonkin, entre Cho-Moi, et That-Khé, leg. Messager (n. 33), RBINS/11; Tonkin, Bac-Kan, RBINS/4; Muong-Kong, leg. Messager, MNHN-IM-2012-2139/1; Secteur de Nac-Ri, Bac-Kan, leg. Messager, MNHN-IM-2012-2250/343; Bac-Kan, leg. Messager, MNHN-IM-2012-2252/60; Bac-Kan, leg. Messager, MNHN-IM-2012-2258/38; That-Khé, coll. Mansuy, MNHN-IM-2012-2259/12; Cho-Moi, leg. Messager, MNHN-IM-2012-2263/48; Bac-Kan, leg. Messager, MNHN-IM-2012-2265/30; Long-Phai, leg. Messager, MNHN-IM-2012-2270/36; Cho-Moi, leg. Messager, MNHN-IM-2012-2275/30; Long-Phai, leg. Messager, MNHN-IM-2012-2277/26; Cho-Moi, leg. Messager, MNHN-IM-2012-2283/95; Cao-Bang, leg. Messager, MNHN-IM-2012-2468/1; Na-Ri, leg. Messager, MNHN-IM-2012-2285/40; Long-Phai, leg. Messager, MNHN-IM-2012-2286/36; Bac-Kan, coll. Letellier, 1949, MNHN-IM-2012-2287/1; Cho-Moi, leg. Messager, MNHN-IM-2012-2300/25; Bac-Kan, coll. Lavezzari, 1929, MNHN-IM-2012-2301/15; Bac-Kan, leg. Messager, MNHN-IM-2012-2305/62; Long-Phai, leg. Messager, MNHN-IM-2012-2312/30; Bac-Kan, coll. Staadt, 1969, MNHN-IM-2012-2313/4; Na-Ri, leg. Messager,

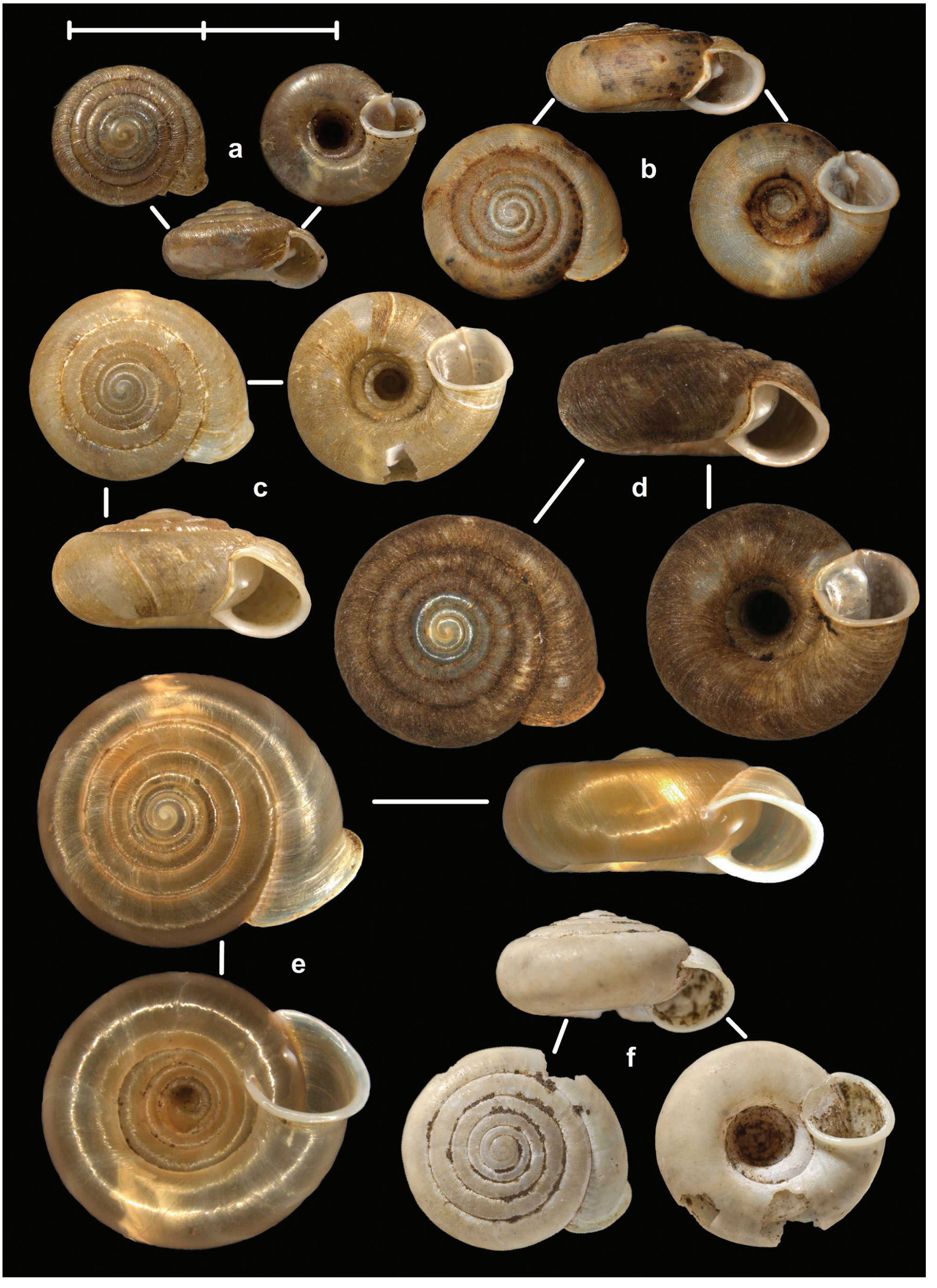

Figure 2. Shells of Vietnamese *Sicradiscus* and *Gudeodiscus* species. **A** *Sicradiscus mansuyi* (Gude, 1908), NHMUK 1907.2.20.19 (syntype) **B** *Gudeodiscus* (*Gudeodiscus*?) *anceyi* (Gude, 1901), Tonkin, Bac-Kan, leg. Messager, MNHN 24600 (syntype) **C** *G.* (*G.*?) *hemmeni* Páll-Gergely & Hunyadi, sp. n., 2012/61, HNHM 97458 (holotype) **D** *G.* (*G.*?) *hemmeni*, Vn10-103 **E** *G.* (*G.*) *fischeri* (Gude, 1901), 20090519B, coll. PGB **F** *G.* (*G.*?) *cyrtochilus* (Gude, 1909), NHMUK 1922.8.29.59. (syntype). Photos: H. Taylor (**A, F**), T. Deli (**B**) and B. Páll-Gergely (**C, D, E**). Scale represents 10 mm.

MNHN-IM-2012-2376/34; Pakhé, leg. Messager, MNHN-IM-2012-2453/1; Tonkin, Bac-Khan, coll. Rolle, 4/11/08, NHMUK 20130585/3; Tonkin, Bac-Khan, coll. Rolle, 4/11/08, NHMUK 20130586/3; Tonkin, Bac-Kan, 13/6/01, NHMUK 20130587/3; Tonkin, Bac-Kan, coll. Rolle, 4/11/08, NHMUK 20130588/3; Tonkin, 4/11/8, NHMUK 20130589/2; Tonkin, Bac-Kan, coll. Salisbury ex Beddome, NHMUK 20130590/2; Tonkin, coll. Lucas, NHMUK 20130591/2; Tonkin, Bac-Khan, NHMUK 1916.03.16.1–2/2; Tonkin, NHMUK 1901.08.01.22/1; Tonkin, NHMUK 1901.7.11.89–90/2; Tonkin, Bac-Kan, coll. Rušnov ex Rolle ex Messager, NHMW 92556/6; Tonkin, Bac-Kan, coll. Wagner ex Messager, NHMW 92557/2; Tonkin, Cho-Moi, coll. Oberwimmer ex. Rosen, NHMW 71640/O/9480/1; Tonkin, Ngam-Son, coll. Wagner ex Messager, NHMW 82558/2; Tonkin, Cho-Moi, coll. Rosen, NHMW 71640/O/9479/2; Tonkin, Bac-Khan, coll. Rolle ex Messager, NHMW 50858/2; Tonkin, That-Khé, entre Cho-Moi, coll. Steenberg, ZMUC-GAS-1809/2.

New material examined. Vn10-33B Bắc Kạn Province, Ba Bể Nat. Park, surroundings of Na Phoong cave, GPS not recorded, leg. Hemmen, Ch. & J., 10.10.2010., PGB/1; **GS21** Bắc Kạn Prov, Na Rì District, left side of road from Kim Hỷ to Bắc Kạn, 2 km after Kim Hỷ, in leaf litter bellow high limestone walls above road, 583 m, 22°16.861'N, 106°2.169'E, leg. Grego, J. & Śteffek, J., 06.04.2012., JG/1; **GS22** Bắc Kạn Prov, Na Rì District, 2 km S of Bản Dền (=Dền Village), limestone rocks at side of the valley near gold quarry, in small cavern in dense rain forest, ca 590 m, 22°14.547'N, 106°0.527'E, leg. Grego, J. & Śteffek, J., 06.04.2012., JG/1, PGB/1; **GS24** Bắc Kạn Prov, Na Rì District, 2 km S of Bản Dền, W slopes of a deep sinkhole covered with forest, leaf litter under high limestone wall, ca 640 m, 22°14.506'N, 106°0.521'E, leg. Grego, J. & Śteffek, J., 06.04.2012., JG/1; **2011/82** Lạng Sơn Province, Lũng Phầy Pass, Thất Khê N 13 km, 475 m, 22°20.363'N, 106°27.098'E, leg. Hunyadi, A., 15.11.2011., HA/4; **2011/91** Bắc Kạn Province, Ba Bể Nat. Park, 500 m on the path starting from the bungalows, 240 m, 22°25.072'N, 105°37.941'E, leg. Hunyadi, A., 17.11.2011., HA/3; **2011/93** Bắc Kạn Province, Ba Bể Nat. Park, Đầu Đẳng Waterfall, above the waterfall, 175 m, 22°27.159'N, 105°34.193'E, leg. Hunyadi, A., 18.11.2011., HA/1; **2011/94** Bắc Kạn Province, Ba Bể Nat. Park, Ao Tiên, near the lake, 155 m, 22°26.831'N, 105°37.023'E, leg. Hunyadi, A., 18.11.2011., HA/3+1jb; **2011/96** Bắc Kạn Province, Ba Bể Nat. Park, Thẩm Kịt Cave 2 km, lookout tower, 335 m, 22°24.686'N, 105°37.710', leg. Hunyadi, A., 19.11.2011., HA/1; **2011/100** Bắc Kạn Province, Ba Bể Nat. Park, Bố Lù, 600 m from the harbour towards Pắc Ngòi, right side of the road, 175 m, 22°23.989'N, 105°37.523'E, leg. Hunyadi, A., 19.11.2011., HA/3; **2011/101** Bắc Kạn Province, Ba Bể Nat. Park, Na Phoong Cave, south of Bố Lù, 215 m, 22°23.341'N, 105°36.812'E, leg. Hunyadi, A., 19.11.2011., HA/3; **2012/45** Bắc Kạn Province, Na Rì Distr., Kim Hỷ SSE, 1.5 km on a by-road from the road nr. 279, 420 m, 22°16.988'N, 106°02.990'E, leg. Hunyadi, A., 29.05.2012., HA/3; **Vn10-68** Cao Bằng Province, right off old rd., ca. 33 km from Cao Bằng to Đông Khê, 22°27.547'N, 106°22.331'E, leg. Hemmen, Ch. & J., 26.03.2010., HE/1; **Vn11-159** Lạng Sơn Province, at km 74.8 on road 1B, Đồng Đăng to Thái Nguyên (8 km S Bắc Sơn), 21°54.543'N, 106°17.298'E, leg. Hemmen, Ch. & J., 02.04.2011., HE/7; **Vn11-31C** Bắc Kạn Province, Ba Bể Nat. Park, near Puổng Cave, 22°27.835'N, 105°38.997'E, leg. Hemmen, Ch. & J., 17.03.2011., HE/1; same data, leg. Hemmen, Ch. & J., 19.10.2009., PGB/2.

Diagnosis. Shell very small, finely ribbed, whole shell with easily-visible spiral lines, spire elevated, umbilicus deep; aperture with well-developed, long apertural fold (Figure 9G). Parietal wall with two lamellae, the anterior is fused with the lower plica, upper plica missing (or short and fused to the anterior lamella); palatal plicae oblique, short, sometimes connected with a ridge (Figures 11C–F).

Measurements (in mm): D = 7.4–7.9, D: 3.5–4 (shells from different localities, n=3); D = 9.2–9.8, H = 4.5–4.6 (Vn11-31C).

Differential diagnosis. *Gudeodiscus messageri* is larger than *G. anceyi* and lacks the apertural fold and spiral lines on the ventral surface of the shell. *Gudeodiscus anceyi* is smaller than typical *G. phlyarius*, has stronger spiral lines, and has no horizontal plica under the lamellae, which are present in most populations assigned to *G. phlyarius*. The *G. phlyarius* populations living near the Chinese border (typical *anterides*, *gouldingi*, *fallax*, *verecunda*) are usually larger than *G. anceyi* and they often lack the apertural fold and the spiral lines on the ventral side of the shell. For differences with *G. hemmeni* sp. n. and *Sicradiscus mansuyi*, see under those species.

Intraspecific diversity. Relatively low; shell characters, namely the size and general shell and aperture shape are rather stable. The morphology of the palatal plicae shows some diversity. The species is easily recognisable and can be separated from other plectopylid species without major problems.

Distribution (see Figure 40): We have newly-collected material only from Bắc Kạn Province. The species was previously recorded from That Khé (Lạng Sơn Province) and Nac Ri (Hà Giang Province) (Gude 1901a, see also Figure 39).

***Gudeodiscus* (*Gudeodiscus*?) *cyrtochilus* (Gude, 1909)**

Figures 2F, 15E–G

1909 *Plectopylis cyrtochila* Gude, Proceedings of the Malacological Society of London, 8: 217–218., Plate 9, Figs 5, 5a–b. [“Muong-Kong”].

2013 *Gudeodiscus cyrtochilus*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 11–12., Figs 17, 41, 75 (map).

Types examined. Tonkin, Muong-Kong, leg. Messager, NHMUK 1922.8.29.59 (syntype, Figure 2F).

Museum material examined. Muong-Kong, coll. Denis 1946, MNHN-IM-2012-2249/3; Muong-Kong, leg. Messager, MNHN-IM-2012-2251/14.

New material examined. 2012/46 Hà Giang Province, Hà Giang 105.2 km towards Đồng Văn, Vân Chải Commune, right side of the road nr. 4C, 23°08.865'N, 105°10.789'E, leg. Hunyadi, A., 31.05.2012., HA/7+4 jb; **2012/47** Hà Giang Province, Hà Giang 105.5 km towards Đồng Văn, Vân Chải Commune, left side of the road 4C, 23°09.084'N, 105°10.774'E, leg. Hunyadi, A., 31.05.2012., HA/19+10jb, PGB/3; **2012/49** Hà Giang Province, Hà Giang 149.4 km towards Mèo Vạc, about 5 km SE from Đồng Văn, right side of the road 4C, ca 1090 m, 23°15.528'N, 105°22.545'E, leg. Hunyadi, A., 01.06.2012., HA/9, PGB/1; **2012/50** Hà Giang Province, Đồng Văn 7.5 km towards Mèo Vạc, left side of the road nr. 4C, 1260 m, 23°14.981'N, 105°23.657'E, leg. Hunyadi, A., 01.06.2012., HA/6jb; **Vn11-141** Hà Giang Province, km 105.5 on road 4c, between Yên Minh and Đồng Văn (NE of Hà Giang town), 23°08.996'N, 105°10.332'E, leg. Hemmen, Ch. & J., 21.03.2011., HE/16; **Vn11-144** Hà Giang Province, km 149.4 on road 4c, between Đồng Văn to Mèo Vạc (NE of Hà Giang Town), 23°15.507'N, 105°22.564'E, leg. Hemmen, Ch. & J., 23.03.2011., HE/4; **Vn11-145** Hà Giang Province, km 153 on road 4c, between Đồng Văn to Mèo Vạc (NE of Hà Giang Town), left side of road, 23°14.738'N, 105°23.786'E, leg. Hemmen, Ch. & J., 23.03.2011., HE/1; **Vn11-123A** Hà Giang Province, ca. 7.5 km from Đồng Văn to Mèo Vạc (right side off road), 23°14.906'N, 105°23.445'E, leg. Hemmen, Ch. & J., 23.03.2011., HE/3.

Diagnosis. Shell very small to small, discoid, polished with very weak apertural rim, weak or missing callus and without apertural fold. Parietal wall with two lamellae and an upper and a lower horizontal plica; the plicae can be free from the anterior lamella or in contact with it; palatal plicae straight, parallel, horizontal, sometimes connected with a slight ridge (Figures 15E–G).

Measurements (in mm): D = 8.9–9.9, H = 4.8–5.0 (n=4, MNHN-IM-2012-2251); D = 10.2–11.1, H = 5.3–5.6 (n=3, 2012/47); D = 10.2–11.2, H = 4.8–5.4. (Chinese specimens, n=4, see Páll-Gergely and Hunyadi 2013).

Differential diagnosis. The Chinese *Gudeodiscus yunnanensis* has a similar shell shape but possesses only one vertical parietal lamella (the anterior one is absent). The two species can be separated only the basis of the presence or absence of the anterior lamella. In *G. soosi* and in most specimens of *G. multispira*, few denticles are present between the upper and lower plicae, at the place of the anterior lamella. Moreover, *G. multispira* has a greater number of whorls and the last whorl is wider in relation to the previous one than in *G. cyrtochilus*. *Gudeodiscus infralevis* is larger with a more elevated spire, stronger apertural lip and usually a weak apertural fold. See also under *G. fischeri*.

Intraspecific diversity. Low; shell characters rather stable. The parietal plicae and lamellae and their respective position (reaching each other or not) show some diversity within the species. The palatal plicae are not variable, but in some shells they are connected to each other with a ridge, whereas in others they are free. It is possible that mature specimens tend to have a connection between the plicae. The species is easily recognisable and can be separated from other plectopylid species without major problems.

Distribution (see Figure 41): The species was described from "Muong-Kong" (=Mường Khương, Lào Cai Province; see Figure 39). Material is noted from northeast of this locality, from northern Hà Giang Province and eastern parts of Yunnan Province (China) (see Páll-Gergely and Hunyadi 2013).

Remarks. The drawing in the original description of *Gudeodiscus cyrtochilus* is incomplete (the posterior lamella was omitted).

Some fresh shells have a characteristic mosaic structure on the dorsal surface (yellowish and darker reddish areas are following each other). This coloration is known in some "*Chersaecia*" (*munipurensis* Godwin-Austen, 1875, *oglei* Godwin-Austen, 1879, *serica* Godwin-Austen, 1875) and *Plectopylis* (e.g. *anguina* Gould, 1847, *bensoni* Gude, 1914, *karenorum* W. Blanford, 1865) species.

***Gudeodiscus* (*Gudeodiscus*) *dautzenbergi* (Gude, 1901)**
Figures 8E–F, 9K–L, 14A–G

1901a *Plectopylis Dautzenbergi* Gude, Journal de Conchyliologie, 49: 198–200., Figs 1a–f. Plate 6, Figs 1a–c. ["That Khé (le type); entre Cho-Moï et Bac-Kan; entre Bac-Kan et Nac-Ri"]
1901a *Plectopylis persimilis* Gude, **syn. n.**, Journal de Conchyliologie, 49: 209–211., Figs 7a–f, Plate 6, Figs 7a–c. ["Environs de That-Khé"].
1959–1960 *Plectopylis schlumbergeri*, — Zilch, Handbuch der Paleozoologie, 6 (2) Euthyneura: Fig. 2094.
2013 *Gudeodiscus dautzenbergi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

Types examined. Tonkin, That-Khé, MNHN 24603 (holotype of *dautzenbergi*, Figure 8E); Environs de That-Khé, leg. Messager (n. 22.), MNHN 24602 (holotype of *persimilis*, Figure 8F).

Museum material examined. Tonkin, Nja-Ba-Thà, coll. Dosch ex Rolle, SMF 341738/1; Tonkin, That-Khé, coll. Dorsch ex Rolle ex Messager, SMF 172083/2; Tonkin, coll. Jetschin ex Bonnet 1900, SMF 102823/1; Fr. Indochina, Tonkin, That Ké, leg. Demange, 1911, HNHM 10278/2; Tonkin, coll. Sayer 1969, MNHN-IM-2012-2273/1; Tonkin, coll. Letellier 1949, MNHN-IM-2012-2274/1; Bac-Kan, leg. Messager 1904, coll. Lavezzari, 1929, MNHN-IM-2012-2290/5; Tonkin, leg. Messager, MNHN-IM-2012-2292/2; Bac-Kan, leg. Messager, MNHN-IM-2012-2297/2; Tonkin, coll. Denis 1946, MNHN-IM-2012-2303/4; Bac-Kan, leg. Messager, MNHN-IM-2012-2314/7; That Khé, leg. Messager, MNHN-IM-2012-2327/4; Bac-Kan, leg. Messager, MNHN-IM-2012-2331/5; Bac-Kan, leg. Messager, MNHN-IM-2012-2437/1; Bac-Kan et That Khé, coll. Staadt 1969, MNHN-IM-2012-2280/2; Na-Ri, leg. Messager, MNHN-IM-2012-2461/1; That-Khé, leg. Messager, MNHN-IM-2012-2373/6; That-Khé, leg. Messager, MNHN-IM-2012-2378/4; Bac-Kan, leg. Messager, MNHN-IM-2012-2382/4; Bac-Kan, leg. Messager, MNHN-IM-2012-2383/4+14jb; Bac-Kan, leg. Messager, MNHN-IM-2012-2402/3; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2336/1; Bac-Kan, leg. Messager, MNHN-IM-2012-2337/26+2jb; That-Khé, leg. Messager, MNHN-IM-2012-2354/4; Cao-Bang, leg. Messager, MNHN-IM-2012-2360/1; Tonkin, That-Khé, coll. Salisbury ex Beddome, Tonkin, coll. Lucas, Acc. no. 2351, NHMUK 20130614/2; Tonkin, coll. Lucas, Acc. no. 2351, NHMUK 20130615/1; Tonkin, coll. Trechmann, Acc.

no. 2176, NHMUK 20130616/2; Tonkin, That Ke (?), coll. Kennard, A. S. ex auct. (Gude), NHMUK 20130617/1; Tonkin, That-Khe, coll. Rolle, 4/11/08, NHMUK 20130618/2; Tonkin, That-Khé, 13/6/03, NHMUK 20130619/2; Tonkin, That-Khé, NHMUK 1901.7.11.1/1; Tonkin, That-Khé, NHMUK 1920.1.20.18/1; Tonkin, That-Khé, NHMUK 1908.12.21.142–143/2; Tonkin, That-Khé, NHMW 46024/1; Tonkin, That-Khé, coll. Rolle, NHMW 92559/2; Tonkin, That-Khé, coll. Oberwimmer, NHMW 71640/O/10285/1; Tonkin, That-Ke, coll. Wagner ex Messager, NHMW 71640/O/10285/1 (mixed sample with *schlumbergeri*); Bac Kan, coll. Steenberg, ZMUC-GAS-1084/1; Tonkin, coll. Steenberg, ZMUC-GAS-1805/2.

New material examined. Vn10-44 Bắc Kạn Province, Chợ Mới (left bank of river); 21°52.682'N, 105°47.078'E, leg. Hemmen, Ch. & J., 17.03.2010., PGB/3; **Vn10-42** Thái Nguyên/Bắc Kạn Province, ca. 1 km S of Chợ Mới; 21°52.707'N, 105°46.172'E, leg. Hemmen, Ch. & J., 17.03.2010., PGB/3; **2011/103** Bắc Kạn Province, Chợ Mới, eastern bank of the river, Khuôn Thung cross 500 m towards Quảng Chu Commune, right side of the road, 21°52.508'N, 105°47.328'E, leg. Hunyadi, A., 21.11.2011., HA/10+4jb, PGB/1; **2011/104** Thái Nguyên Province, Chợ Chu (=Chu Market), rocky wall above the NE part of the village, 90 m, 21°54.613'N, 105°39.195'E, leg. Hunyadi, A., 21.11.2011., HA/3.

Diagnosis. Shell medium-sized or large, with irregular growth lines, but appearing almost smooth; spire slightly elevated, apertural lip thick but blunt; apertural fold strong and oblique, connected to the callus, but reaching its maximum height some distance from the callus (Figures 9K–L). Parietal wall with two parietal lamellae; the anterior one has an anteriorly conspicuously elongated lower "leg"; this structure may have resulted from the connection of the anterior lamella and the lower plica; middle palatal plicae oblique (Figures 14A–G).

Measurements (in mm): D = 16.7–20.6, H = 8.9–9.8 (n=3, Vn10-42); D = 16.1–17.8, H = 7.9–9.2 (n=2, Vn10-44).

Differential diagnosis. *Gudeodiscus villedaryi*, which is probably the closest relative, differs from *G. dautzenbergi* by the presence of an additional horizontal parietal plica under the vertical lamellae, near the suture. Distinguishing *G. dautzenbergi* from some similar looking populations of *G. villedaryi* is impossible without breaking the shell and observing the parietal plicae. Most populations of *G. villedaryi* however, have a sharp periumbilical keel, which always absent in *G. dautzenbergi* (see also Remarks under *G. villedaryi*). *Gudeodiscus dautzenbergi* is flatter and more widely umbilicated than *G. giardi*. The latter species has a domed shell, thinner shell wall and thicker peristome. For comparisons with *Halongella schlumbergeri*, see under that species. Distinguishing *G. dautzenbergi* from *H. schlumbergeri* requires experience, but is possible without breaking the shell on the basis of the formation of the peristome and the apertural fold (Figures 9K–N).

Intraspecific diversity. Low; shell characters stable.

Distribution (see Figure 40): This species as well as *Plectopylis persimilis* (synonym of *Gudeodiscus dautzenbergi*) were described from That-Khé (northern Lạng Sơn Province) (see Figure 39). Our newly-collected material is from the border region of the Thái Nguyên and Bắc Kạn provinces.

Remarks. The holotype of *Plectopylis persimilis* and that of *Plectopylis dautzenbergi* do not show significant differences in terms of shell shape, size, aperture shape and the formation of the plicae and lamellae; therefore we synonymise *Plectopylis persimilis* with *P. dautzenbergi*. These two species were described in the same publication (Gude 1901a), therefore the name introduced earlier (*dautzenbergi*, page 198) is considered a senior synonym.

Gudeodiscus dautzenbergi and *G. villedaryi* are separated here on the basis of the presence or absence of a lower plica, although the two species may be conspecific. More information is necessary to clarify the distinctness of *G. dautzenbergi*.

The specimen figured by Zilch (1960, Fig. 2094) under the name *Plectopylis* (*Endoplon*) *schlumbergeri* is missing. There is a note written by Zilch saying that he found the box empty on 11.12.1963 (Ronald Janssen, pers. comm., October 2013). Although the specimen could not be examined by us, we are confident in stating that the figure shows a shell of *Gudeodiscus dautzenbergi*.

***Gudeodiscus* (*Gudeodiscus*) *fischeri* (Gude, 1901)**

Figures 2E, 3A–C, 9P–Q, 15H–R, 17, 18, 28D, 29D, 29J, 30E, 31D, 34M–O

1901a *Plectopylis Fischeri* Gude, Journal de Conchyliologie, 49: 204–205., Figs 4a–e, Plate 6, Figs 4a–c. [“Environs de Bac-Kan”].

1901a *Plectopylis tenuis* Gude, **syn. n.**, Journal de Conchyliologie, 49: 202–204, 205., Figs 3a–e, Plate 6, Figs3 a–c. [“Cho-Ra (le type); environs de Bac-Khan; environs de Cho Moi”].

1905b *Plectopylis Fischeri*, — Dautzenberg & Fischer, Journal de Conchyliologie, 53: 360. [“Ha Giang”].

1909 *Plectopylis tenuis*, — Gude, Proceedings of the Malacological Society of London, 8: 215, 216.

2013 *Gudeodiscus fischeri*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

2013 *Gudeodiscus tenuis*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

Types examined. Tonkin, Environs de Bac-Kan, leg. Messager, MNHN 24579 (holotype of *fischeri*, Figure 3B); Tonkin, Cho-Ra, leg. Messager, MNHN 24587 (holotype of *tenuis*, Figure 3C).

Museum material examined. Tonkin, Bac-Kan, NHMUK 1908.12.21.144/1; Tonkin, environs de Bac-Kan, leg. Messager, (n. 28), RBINS/2; Tonkin, Ha-Giang, leg. Messager, RBINS/5; Ha Giang, leg. Mansuy, coll. M. H. Fischer, MNHN-IM-2012-2241/12 adult, 1jb; Ha Giang, coll. Mansuy, MNHN-IM-2012-2257/5; Tonkin, leg. Messager, MNHN-IM-2012-2390/1; Cho-Ra, leg. Messager, MNHN-IM-2012-2477/1; Bac-Kan, leg. Messager, MNHN-IM-2012-2466/3; Tonkin, Cho Rah, ex Rolle, USNM 207813/2 („*tenuis*“); Nga-Son, leg. Messager, MNHN-

Figure 3. Shells of Vietnamese *Gudeodiscus* species. **A** *Gudeodiscus* (*Gudeodiscus*) *fischeri* (Gude, 1901), Vn10-120, coll. PGB **B** *G.* (*G.*) *fischeri*, MNHN 24579 (holotype of *Plectopylis fischeri*) **C** *G.* (*G.*) *fischeri*, MNHN 24587 (holotype of *Plectopylis tenuis*) **D** *G.* (*G.?*) *infralevis* (Gude, 1908), MNHN 24604 (holotype of *Plectopylis infralevis*) **E** *G.* (*G.?*) *infralevis*, MNHN 24585 (holotype of *Plectopylis soror*). Photos: B. Páll-Gergely (**A**) and T. Deli (**B–E**). Scale represents 10 mm.

IM-2012-2233/2 („*tenuis*"); Nga-Son, leg. Messager, MNHN-IM-2012-2253/2 ("*tenuis*"); Tonkin, coll. Denis, 1946, MNHN-IM-2012-2338/3 ("*tenuis*"); Cho-Ra, leg. Messager, MNHN-IM-2012-2361/1 ("*tenuis*"); Tonkin, Bac-Kan, coll. Rolle, NHMW 71640/O/14028/1.

New material examined. 20090519B Tuyên Quang Province, Hàm Yên District, Yên Phú Commune, Đồng Tiến, Thống Nhất, ca 70 m, 22°08.673'N, 104°58.634'E, leg. Ohara, K., 19.05.2009., OK/12, PGB/3; **20090515C** Bắc Kạn Province, Ba Bể District, Ba Bể Nat. Park, Khâu Kum, ca 185 m, 22°26.465'N, 105°36.642'E, leg. Ohara, K., 15.05.2009., OK/8, PGB/2; **20081113C** Hà Giang Province, Hà Giang Town, Ngọc Đường Commune, Bản Cườm (= Cườm Village), ca 110 m, 22°51.180'N, 105°01.075'E, leg. Ohara, K., 13.11.2008., OK/1, PGB/1; **Vn10-118** Hà Giang Province, Tâm Village, ca. 7–8 km SE of Hà Giang (between Vị Xuyên and Bản Hăm = "Hăm Village"), 22°48.019'N, 105°00.888'E, leg. Hemmen, Ch. & J., 16.10.2010., PGB/2; **Vn11-138** Tuyên Quang Province, near Tôn Hông, road #185 from Tuyên Quang to Vĩnh Lộc (formerly Chiêm Hóa) (NE of Tuyên Quang), leg. Hemmen, Ch. & J., 19.03.2011., HE/1, PGB/1 (anatomically examined, see Figures 17, 28D, 29J, 31D, 34M–O); **Vn10-120** Hà Giang Province, ca. 9.8 km from Hà Giang to Tam Sơn (formerly Quản Bạ), left side off road, 22°52.907'N, 104°59.885'E, leg. Hemmen, Ch. & J., 17.10.2010., PGB/3; **2012/56** Hà Giang Province, Hà Giang 7 km towards Tam Sơn, left side of the road nr. 4C, 100 m, 22°51.650'N, 105°00.768'E, leg. Hunyadi, A., 03.06.2012., HA/4; **2012/57** Hà Giang Province, Hà Giang 9.8 km towards Tam Sơn, left side of the road 4C, 120 m, 22°52.881'N, 104°59.927'E, leg. Hunyadi, A., 03.06.2012., HA/20+7jb, PGB/2; **Vn11-179** Tuyên Quang Province, ca. 5.5 km E of Chương Dương (left bank of Lô River), leg. Hemmen, Ch. & J., 30.09.2011., HE/2; **20090517A** Bắc Kạn Province, Ba Bể District, Ba Bể Nat. Park, along the trekking road, near guest house, 205 m, 22°25.049'N, 105°37.699'E, leg. Ohara, K., 17.05.2009., OK/8, PGB/2 ("*tenuis*", anatomically examined, see Figure 29D); **Vn10-28A** Bắc Kạn Province, ca 1 km from Ba Bể Nat. Park, headquarters to Ba Bể Lake, 22°24.829'N, 105°37.652'E, leg. Hemmen, Ch. & J., 20.10.2010., PGB/6 ("*tenuis*"); **Vn09-26** Bắc Kạn Province, Ba Bể Nat. Park, near bungalows (at Park Headquarters), leg. Hemmen, Ch. & J., 17.10.2009., HE/2 ("*tenuis*"); **2011/91** Bắc Kạn Province, Ba Bể Nat. Park, path starting from the bungalows 500 m, 240 m, 22°25.072'N, 105°37.941'E, leg. Hunyadi, A., 17.11.2011., HA/11+5jb, PGB/2 ("*tenuis*"); **2011/96** Bắc Kạn Province, Ba Bể Nat. Park, Thẳm Kịt Cave 2 km from the look-out tower, 335 m, 22°24.686'N, 105°37.710'E, leg. Hunyadi, A., 19.11.2011., HA/29+3jb, PGB/2 ("*tenuis*", anatomically examined, see Figure 18); **2011/97** Bắc Kạn Province, Ba Bể Nat. Park, Thẳm Kịt Cave 1 km from the look-out tower, no GPS data, leg. Hunyadi, A., 19.11.2011., HA/8+4jb ("*tenuis*").

Diagnosis. Shell small to medium-sized, with smooth basal and usually finely ribbed apical surface (in some populations also smooth and glossy, see Figure 2E); shell usually flat, or with very slightly elevated spire, or only the protoconch is elevated from the dorsal surface; callus and apertural fold (if present) weak (Figures 9P–Q). Parietal wall with two lamellae (the anterior is exceptionally dissolved into small denticles);

middle palatal plicae oblique, depressed Z or L-shaped, they are free or sometimes connected to each other (Figures 15H–N).

Measurements (in mm): D = 16.6–18.6, H = 7–7.9 (n=3, Vn10-120); D = 12.1–12.4, H = 4.8–5.3 (n=3, 20090519B); D = 15.5–15.9, H = 7.1–7.2. (n=2, 20090515C); D = 14.6, H = 7.4–7.6. (n=2, 2011/91); D = 12.9–14.7, H = 6.4–7.3 (n=6, Vn10-28A).

Differential diagnosis. *Gudeodiscus cyrtochilus* is smaller than *G. fischeri*, it has a narrower umbilicus, more regularly growing whorls (the last whorl is only slightly wider than the penultimate one), a shorter lower horizontal parietal plica and no apertural fold. The Chinese *G. multispira* and *G. soosi* are also smaller, have a greater number of densely-coiled whorls and at the position of the anterior lamella there are usually 2–4 clearly separated denticles (see also Remarks). In some populations of *G. multispira* the denticles are missing so that only the posterior lamella is present. *Gudeodiscus yunnanensis* has no anterior lamella, just a curved single lamella (homologous with the posterior lamella). *Gudeodiscus eroessi* never has an apertural fold and its anterior lamella is dissolved into small denticles, or missing. *Gudeodiscus infralevis* and *G. suprafilaris* have a more elevated spire, narrower umbilicus and rather straight, horizontal, parallel plicae.

Intraspecific diversity. The variability is quite large in terms of shell size and shape, sculpture, strength of the callus and apertural fold and the formation of parietal plicae and lamellae. The combination of weak callus and apertural fold and the "nautiliform" shape helps in the identification of the species. See also Table 7.

Description of the genitalia. Two specimens were dissected, belonging to two different populations: "Specimen1" Tuyên Quang Province, near Tôn Hông, road #185 from Tuyên Quang to Vĩnh Lộc (formerly Chiêm Hóa) (NE of Tuyên Quang), leg. Hemmen, Ch. & J., 19.03.2011. (specimen without embryos in the uterus, but with calcareous hooks inside the penis, Figure 17, 31D); "Specimen2" Bắc Kạn Province, Ba Bể Nat. Park, Thẳm Kịt Cave 2 km from the look-out tower, 335 m, 22°24.686'N, 105°37.710'E, leg. Hunyadi, A., 19.11.2011. (typical *Plectopylis tenuis*; with a developing embryo in the uterus, Figure 18).

The penis is a cylindrical tube with several longitudinal, parallel folds on the inner wall; there are pockets formed by some of these folds; in the wall of the opened penis the series of pockets are arranged along a bell-shaped line (Figure 28D); there were calcareous hooks within the pockets of "Specimen1"; the base of the hooks were elongated, they lay within the pockets, whereas the tip portion projects out of the pockets (Figure 30E); epiphallus as long as the penis, with few parallel folds in the lumen (Figure 29D); distal portion of the penis and the proximal part of the epiphallus are connected with weak membrane; more closely to the genital opening these two organs are more stronger connected; penial caecum tapers toward the end, it is about a quarter as long as the penis; its inner wall with irregular folds arranged in longitudinal lines, with calcareous granules in between (mainly at the distal end); retractor muscle attaching on the apical part of the penial caecum is approximately as long as the caecum; there is an additional retractor muscle on the proximal part of the penis. Vagina is thickened and forms a "vaginal bulb", which is attached to the body wall with several thin ligaments; inner wall of the vaginal bulb and the distal part of the vagina with well-developed,

Table 7. Diversity of shell characters within the species *Gudeodiscus* (*Gudeodiscus*) *fischeri*. Abbreviations: OAE: only apex elevated.

code	callus and apertural fold	anterior lamella	lamella and lower plica	shells opened	shell	spire	remarks
2012/57= Vn10-120	strong	dissolved	not in contact	2	thick, greyish	slightly elevated	large
2012/56	strong	normal	connected	1	thick, greyish	slightly elevated	
20081113C	strong	normal	connected	1	thick, greyish	slightly elevated	
Vn10-118	strong	normal	connected	1	thick, greyish	OAE	
20090515C	weak	normal	connected	2	thin, translucent, corneous	slightly elevated	typical *fischeri*
20090519B	weak	normal	connected	2	very thin, translucent, yellowish	OAE	small
2011/96= 2011/91= 2009.05.17A= Vn10-28A	weak	normal	not in contact	5	thin, translucent, corneous	elevated	typical *tenuis*

longitudinal, serrulate folds (Figure 31D); stem of the gametolytic sac is long and slim; it is attached hardly to the spermoviduct; diverticulum well-developed, free; the diverticulum of the specimen from the Ba Bể Nat. Park contained three long, slightly C-shaped spermatophores; the proximal side of the spermatophores were damaged, thus they might have been connected; spermoviductus slim and long.

Besides the presence or absence of embryos and calcareous penial hooks between the two specimens the only notable difference is the longer retractor muscle in "Specimen2" than in "Specimen1", but the taxonomic value of this character is unknown.

Radula. See Table 6 and Figures 34M–O.

Distribution (see Figure 41): *Gudeodiscus fischeri* is known from Hà Giang, Tuyên Quang and Bắc Kạn Provinces.

Remarks. Some samples from the Ba Bể Nat. Park (Vn10-28A, 20090517A, 2011/91, 2011/96) are identical with the type specimen of *Plectopylis tenuis* described from Cho Ra (see Figure 39). This town is situated approximately 7 km from the locality of our recent material. Some 3 km north of our *tenuis* localities there is a population (20090515C) which agrees with *tenuis* in every shell character except that the anterior parietal lamella and the lower horizontal plica are connected (typical in *fischeri*). Since no other shell characters are known to be different between *tenuis* and *fischeri*, and other populations of *fischeri* show relatively large variability in terms of several shell characters, we synonymize *Plectopylis tenuis* with *P. fischeri*.

The shells collected 9.8 km north of Hà Giang are relatively large and thick-walled, have the anterior lamella dissolved into 3–4 denticles, and have strong apertural denticle and callus (Figures 3A, 15L–M). The shells collected at Đồng Tiến are small and very glossy in appearance (Figure 2E).

***Gudeodiscus* (*Gudeodiscus*?) *francoisi* (Fischer, 1898)**

Figures 7A–C, 13E–K

1898b *Plectopylis Françoisi* Fischer, Journal de Conchyliologie, 46: 214–218., Figs 1, 3–4. ["rochers calcaires Déo-Ma-Phuc"].
1899 *Plectopylis Françoisi* Fischer, Bulletin biologique de la France et de la Belgique, 32: 330–332., Figs 1, 3–4. ["rochers calcaires Déo-Ma-Phuc"].
1899b *Plectopylis françoisi*, — Gude, Science Gossip, 6: 75–76., Figs 201a–e.
1899c *Plectopylis* (*Endoplon*) *françoisi*, — Gude, Science Gossip, 4: 148.
1899d *Plectopylis* (*Endoplon*) *françoisi*, — Gude, Science Gossip, 6: 175.
1900 *Plectopylis lepida* Gude, **syn. n.**, The Annals and Magazine of Natural History, 7 (5): 313. ["Tonkin, Tinh-Tuc"].
1901a *Plectopylis Bavayi* Gude, **syn. n.**, Journal de Conchyliologie, 49: 200–202., Figs 2a–e, Plate 6, Figs 2a–c. [That Khé (le type); secteur de Nac-Ri].
1901b *Plectopylis lepida*, — Gude, Journal of Malacology, 8: 48–49., Figs 4a–f.
1908 *Plectopylis Bavayi*, — Dautzenberg & Fischer, Journal de Conchyliologie, 56: 177. [Quang-Huyen].
2013 *Gudeodiscus francoisi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 8.
2013 *Gudeodiscus lepidus*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 8.

Types examined. Rochers calcaires de Déo-Ma-Phuc, leg. Dr. Billet, 23.10.1892, MNHN 9945 (holotype of *francoisi*, Figure 7B); That-Khé, leg. Messager, MNHN 24601 (holotype of *bavayi*, Figure 7A); Tonkin, Tinh-Tuc, NHMUK 1922.8.29.51 (holotype of *lepida*, Figure 7C).

Museum material examined. Tonkin, coll. Jetschin ex Bonnet 1900, SMF 102826/1; Tonkin, That Khé, coll. Dosch ex Rolle, SMF 172090/4; Tonkin, That-Khé, coll. Dosch ex Rolle, SMF 172082/2; Tonkin, leg. Messager, MNHN-IM-2012-2227/6; Tonkin, leg. Messager, MNHN-IM-2012-2229/4; Tonkin, coll. Letellier 1949, MNHN-IM-2012-2267/1; Secteur de Nac-Ri, leg. Messager, MNHN-IM-2012-2268/5; That-Khé, coll. Lavezzari, 1929, MNHN-IM-2012-2276/5; Tonkin, leg. Messager, MNHN-IM-2012-2284/1; That Ké, Nac Ri, leg. Messager, MNHN-IM-2012-2333/8; Tonkin, leg. Messager, MNHN-IM-2012-2353/1; Na-Cham, leg. Messager, MNHN-IM-2012-2358/5; Na-Ri, leg. Messager, MNHN-IM-2012-2363/5; Tonkin, leg. Messager, MNHN-IM-2012-2428/1; Tonkin, leg. Messager, MNHN-IM-2012-2440/6; Tonkin, leg. Messager, MNHN-IM-2012-2430/7; Nac-Ri et That-Khe, coll. Staadt, 1969, MNHN-IM-2012-2386/2; Tonkin, leg. Messager, MNHN-IM-2012-2371/3; That-Khé, leg. Messager, MNHN-IM-2012-2377/30+3jb; Tonkin, That-Khé, coll. Salisbury ex Beddome, NHMUK 20130592/2; Tonkin, coll. Kennard, A. S. ex auct. (Gude), NHMUK 20130593/2; Tonkin, coll. Lucas, Acc. no. 2351, NHMUK 20130594/2; Tonkin, coll. Lucas, Acc. no. 2351, NHMUK 20130595/2; Tonkin, That-Khé, V.W. MacAndrew Coll, 13/6/01.114, NHMUK 20130596/2; Tonkin, NHMUK 1916.3.15.4–5/2 ("showing immature armature"); Tonkin, That Khé, NHMUK 1901.7.11.46/1; Tonkin, That-Khé, NHMUK 1908.12.21.118–119/2; Baie d'Along, coll. Staadt, 1969, MNHN-IM-2012-2311/1 (similar to the holotype of *Plectopylis lepida*); Tonkin, That-Khe Na-Ri, coll. Rušnov ex Rolle ex Messager, NHMW 92561/2; Tonkin, Phi-Mi, coll. Steenberg, ZMUC-1807/1; Tonkin, coll. Steenberg, ZMUC-GAS-1806/1; Tonkin, coll. Steenberg, ZMUC-GAS-1810/1.

New material examined. GS17 Bắc Kạn Province, Na Rì Distr., limestone cliffs on the left side of the road to Kim Hỷ, 2 km before Kim Hỷ, soil in small cavern, ca 560 m, 22°16.897'N, 106°2.754'E, leg. Grego, J. & Śteffek, J., 05.04.2012., JG/1, PGB/1; **GS22** Bắc Kạn Province, Na Rì District, 2 km S of Bản Dền (=Dền Village), limestone rocks at side of the valley near gold quarry, in small cavern in dense rain forest, ca 590 m, 22°14.547'N, 106°0.527'E, leg. Grego, J. & Śteffek, J., 06.04.2012., JG/1; **GS24** Bắc Kạn Prov, Na Rì Distr., 2 km S of Bản Dền, W slopes of a deep sinkhole covered with forest, leaf litter under high limestone wall, ca 640 m, 22°14.506'N, 106°0.521'E, leg. Grego, J. & Śteffek, J., 06.04.2012., JG/1, PGB/2; **2011/80** Cao Bằng Province, Đèo Mã Phục (pass) 1 km towards Quảng Uyên, right side of the road, 565 m, 22°43.918'N, 106°20.490'E, leg. Hunyadi, A., 14.11.2011., HA/2+2jb; **2012/41** Cao Bằng Province, Đèo Mã Phục (pass) 1 km towards Quảng Uyên, right side of the road, 570 m, 22°43.896'N, 106°20.484'E, leg. Hunyadi, A., 27.05.2012., HA/11+2jb, PGB/2.

Diagnosis. Shell small to medium-sized, yellowish or mustard-coloured, glossy, with slowly increasing whorls, deep umbilicus, domed dorsal side; thin apertural lip and well-developed apertural fold. Parietal wall with two parietal lamellae; the anterior one is connected to the lower plica; middle palatal plicae oblique, depressed Z-shaped (Figures 13E–K).

Measurements (in mm): D = 13.2, H = 6.7 (holotype of *lepida*); D = 19.6–19.8, H = 10.4–10.7 (N = 2, NHMUK 20130593); D = 17.8–18.0, H = 9.8–9.9 (n=2, NHMUK 1908.12.21.118–119).

Differential diagnosis. The glossy, dark yellow shell, the characteristic apertural fold and shell shape makes this species easily distinguishable from most congeners. *Gudeodiscus francoisi* has a smoother shell, weaker apertural lip and more regular whorls than *G. giardi giardi*. In the type locality of *francoisi* (Déo-Ma-Phuc, see Figure 39) the species lives together with *G. giardi giardi*. In some cases the two species can be hardly distinguished, especially in the case of subadult *giardi* specimens which cannot be easily distinguished from *francoisi*. The possibility of hybridisation in that locality cannot be excluded; however specimens from other localities are easily distinguishable.

Intraspecific diversity. The species shows little intraspecific variability in terms of shell characters. The "*lepida*-like" shells are considered to the results of abnormal growth.

Distribution (see Figure 42): Newly-collected material from Cao Bằng and Bắc Kạn Provinces was examined. There is a single shell which is identical to the holotype of *Plectopylis lepida* and is labelled as being collected from Hạ Long Bay, but this collection locality is probably incorrect.

Remarks. *Gudeodiscus bavayi* is a synonym of *G. francoisi*. The two holotypes are identical in shell shape and arrangement of the inner lamellae. The only difference is that the holotype of *G. francoisi* lacks an apertural fold because it is a subadult shell. Other shells collected from the type locality are identical with the holotype of *Plectopylis bavayi*. *Plectopylis lepida* was described on the basis of a single shell. During the revision of the Vietnamese Plectopylidae material in the MNHN, we found a single shell (Baie d'Along, coll. Staadt, 1969, MNHN-IM-2012-2311) which is identical in shell shape and plication with the holotype of *lepida*. These two shells differ from *G. francoisi* only by the absence of the posterior lamella and the weak apertural fold. The absence of the posterior lamella is probably the result of unusual development, which is also visible in a specimen of *G. suprafilaris* (see under that species). The weak apertural fold can be explained by subadult stages of these shells. Since no other shell characters distinguish *Plectopylis lepida* and *G. francoisi*, the former is treated as a junior synonym of *Plectopylis francoisi*.

***Gudeodiscus* (*Gudeodiscus*) *giardi giardi* (Fischer, 1898)**

Figures 7E–F, 8A, 9I, 13L–U, 19, 28B, 29E, 30D, 32C, 35A–C, 45A

1898a *Plectopylis Giardi* Fischer, Bulletin Biologique de la France et de la Belgique, 28: 320–322., Plate 17, Figs 17–21. ["Cao-Bang"].

1898b *Plectopylis Giardi* Fischer, Journal de Conchyliologie, 46: 214–218., Figs 2, 5–6. ["rochers calcaires Déo-Ma-Phuc"].

1899 *Plectopylis Giardi* Fischer, Bulletin Biologique de la France et de la Belgique, 32: 330–332., Figs 2, 5–6.

1899a *Plectopylis giardi*, — Gude, Science Gossip, 5: 332–333., Figs 95a–e ["Cao-Bang, Tonkin"].

1899a *Plectopylis congesta* Gude, **syn. n.**, Science Gossip, 5: 332–333., Figs 96a–f ["Tonkin", "Its exact locality, unfortunately, was not stated."].

1899b *Plectopylis giardi*, — Gude, Science Gossip, 6: 76., Fig. 103.

1899c *Plectopylis* (*Endoplon*) *giardi*, — Gude, Science Gossip, 4: 148.

1899c *Plectopylis* (*Endoplon*) *congesta*, — Gude, Science Gossip, 6: 148.

1899d *Plectopylis* (*Endoplon*) *giardi*, — Gude, Science Gossip, 6: 175.

1899d *Plectopylis* (*Endoplon*) *congesta*, — Gude, Science Gossip, 6: 175, 176.

1901a *Plectopylis congesta*, — Gude, Journal de Conchyliologie, 49: 199, 202, 209, 211–212. ["Entre Bac-Kan, et Nac-Ri; environs de Bac-Kan; That-Khé"].

1908 *Plectopylis Giardi*, — Gude, Journal de Conchyliologie, 55: 346–348., Figs 1a–b ["Cao-Bang", "Quang-Huyen"].

2013 *Gudeodiscus congestus*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

2013 *Gudeodiscus giardi giardi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 19–20., Figs 28, 53a–b, 58 (map).

Types examined. Haut-Tonkin, Cao-Bang, leg. Billet, M., MNHN 9946 (2 syntypes of *giardi*, Figure 8A); Vietnam, Tonkin, environs de Bac-Kan, leg. Messager, MNHN IM-2010-12120 (syntype of *congesta*, Figure 8E); Vietnam, Tonkin, environs de Bac-Kan. leg. Messager, NHMUK 1922.8.29.49 (syntype of *congesta*, Figure 8F).

Museum material examined. Tonkin, coll. Jetschin ex Bonnet 1900, SMF 341736/2; Tonkin, Möllendorff ex Fulton, SMF 150136/1; Tonkin, coll. Jetschin ex Berlier 1908, SMF 102817/1; Tonkin, environs de Bac-Kan, leg. Messager (n. 28), RBINS/1; Tonkin, Long-Phai, NHMSB 122815/1; Long-Phai, leg. Messager, 1901, MNHN-IM-2012-2231/13; Nga-Son, leg. Messager, MNHN-IM-2012-2235/1; Long-Phai, leg. Messager, 1901, MNHN-IM-2012-2236/16; Quang-Huyen, leg. Mansuy, MNHN-IM-2012-2238/14; Bac-Kan, leg. Messager, MNHN-IM-2012-2239/7; That-Khé, leg. Messager, MNHN-IM-2012-2240/9; Bac-Kan, leg. Messager, MNHN-IM-2012-2246/8; Quang-Huyen, Ha-Lang, Coll. Mansuy, MNHN-IM-2012-2248/14; That-Khé, coll. Letellier 1949, MNHN-IM-2012-2266/1; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2278/1; Tonkin, coll. Letellier, 1949, MNHN-IM-2012-2293/1; Tonkin, coll. Mansuy, MNHN-IM-2012-2298/1; Entre Bac-Kan et Nac-Ri, coll. Lavezzari, 1929, MNHN-IM-2012-2302/6; Tonkin, coll. Letellier, 1949, MNHN-IM-2012-2308/1; Tonkin, coll. Levazzari, 1929, MNHN-IM-2012-2309/3; That-Khé, leg. Messager, MNHN-IM-2012-2310/6; Cao-Bang, leg. Messager, MNHN-IM-2012-2469/7; Tonkin, leg. Messager, MNHN-IM-2012-2460/9; Tonkin, leg. Messager, MNHN-IM-2012-2441/1; Halong Bay, leg. Messager, MNHN-IM-2012-2318/1; Halong Bay, leg. Messager, MNHN-IM-2012-2319/1; Halong Bay, leg. Messager, MNHN-IM-2012-2323/1; Tonkin, Bac-Kan, Na-Ri, leg. Messager, MNHN-IM-2012-2324/47; That Khé, leg. Messager, MNHN-IM-2012-2326/3; Po Ma, leg. Messager, MNHN-IM-2012-2328/7; That Khé, coll. Staadt 1969, MNHN-IM-2012-2330/3; That Khé, leg. Messager, MNHN-IM-2012-2341/28; Po Ma, leg. Messager, MNHN-IM-2012-2342/6; Col de Nuages, leg. Messager, MNHN-IM-2012-2343/4; Bac-Kan, leg. Messager, MNHN-IM-2012-2344/8; Tonkin, leg. Messager, MNHN-IM-2012-2345/8; That Khé, leg. Messager, MNHN-IM-2012-2346/5; Cold de Nuages, leg. Messager, MNHN-IM-2012-2349/4; Quang-Huyen, coll. Staadt, 1969, MNHN-IM-2012-2351/1; Tonkin, leg. Messager, MNHN-IM-2012-2352/10; Tonkin, leg. Messager, MNHN-IM-2012-2355/1; Na-Cham, leg. Messager, MNHN-IM-2012-2356/10; Na-Cham, leg. Messager, MNHN-IM-2012-2357/5; Cao-Bang, leg. Messager, MNHN-IM-2012-2359/4; That-Khé, leg. Messager, MNHN-IM-2012-2374/4; Tinh Tuc, secteur de Nguyen Binh, coll. Achat Boubée, MNHN-IM-2012-2385/1; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2393/1; Tonkin, coll. Jousseaume, MNHN-IM-2012-2399/1; Bac-Kan, leg. Messager, MNHN-IM-2012-2432/1; Tonkin, leg. Messager, MNHN-IM-2012-2426/3; Bac-Kan, leg. Messager, MNHN-IM-2012-2435/1; Tonkin, coll. Lucas, Acc. no. 2351, NHMUK 20130604/2 (under the name "*persimilis*"); Tonkin, 3/10/08, NHMUK 20130605/2 (under the name "*persimilis* v. *minor*"); Tonkin, That-Khé, 3/10/08, NHMUK 20130606/3 (under the name "*persimilis*"); Tonkin, coll. Lucas, Acc. no. 2351, NHMUK 20130607/1; Tonkin, 27/6/00, 28, NHMUK 20130608/3 ("*congesta*"); Tonkin, Phi-Mi, coll. Salisbury ex Beddome, NHMUK 20130609/2 ("*congesta*"); Tonkin, coll. Kennard, A. S. ex Gude, NHMUK 20130610/1 ("*congesta*"); Tonkin, Quang-Huyen, NHMUK 1916.3.16.21/1; Tonkin, Quang-Huyen, NHMUK 1907.2.20.17–18/2; Haut-Tonkin, NHMUK 1904.8.1.1–2/2 (under the name "*persimilis*"); Tonkin, That-Khé, NHMUK 1900.2.13.221/1; Tonkin, That-Khé, NHMUK 1920.1.20.17/1; Tonkin, Long-Phai, coll. Wagner ex Messager, NHMW 71640/O/10289/1; Tonkin, Ngan-Son, coll. Wagner ex Messager, NHMW 71640/O/10288/1; Tonkin, Phi-Mi, NHMW 46023/2; Tonkin, Long-Phai, NHMW 46294/2; Tonkin, That-Khe, coll. Wagner ex Messager, NHMW 71640/O/10286/1; Tonkin, Po-Ma (?), coll. Wagner ex Messager, NHMW 71640/O/10287/1; Tonkin, Bac-Khuon, coll. Rolle, NHMW 103352/1 (mixed sample with *phlyarius*); Tonkin, Quang-Huyen, coll. Steenberg, ZMUC-GAS-1813/2.

New material examined. Vn10-58 Cao Bằng Province, ca. 31.5 km from Phục Hòa to Mã Phục (left off rd.), 22°42.212'N, 106°22.055'E, leg. Hemmen, Ch. & J., 20.3.2010., PGB/1; **Vn10-61** Cao Bằng Province, ca. 2 km from Quảng Uyên to Hạ Lang (right off rd.) 22°42.685'N, 106°27.232'E, leg. Hemmen, Ch. & J., 24.3.2010., PGB/2; **Vn10-59** Cao Bằng Province, ca. 30 km from Phục Hòa to Mã Phục (right off rd.), 22°41.787'N, 106°22.652'E, leg. Hemmen, Ch. & J., 23.3.2010., PGB/3; **Vn09-23** Cao Bằng Province, ca. 4.5 km from Mã Phục to Cao Bằng (NW of Cao Bằng), ca. 400 m, 22°42.814'N, 106°19.630'E, leg. Hemmen, Ch. & J., 16.10.2009., PGB/4; **Vn10-57** Cao Bằng Province, ca. 4.5 km from Mã Phục to Cao Bằng (left off rd.), 22°42.661'N, 106°19.627'E, leg. Hemmen, Ch. & J., 23.03.2010., PGB/3; **20081115D** Cao Bằng Province, Hòa An District, Nguyễn Huệ Commune, Hạ Lang, ca 390 m, 22°42.703'N, 106°19.606'E, leg. Ohara, K., 15.11.2008., OK/6, PGB/1; **20081116C** Cao Bằng Province, Trùng Khánh District, Cảnh Tiên Commune, Pắc Rảo., ca 545 m, 22°48.941'N, 106°30.549'E, leg. Ohara, K., 16.11.2008., OK/7, PGB/2; **Vn10-69** Cao Bằng Province, ca. 34.5 km from Cao Bằng to Đông Khê (left off new rd.), 22°27.439'N, 106°24.994'E, leg. Hemmen, Ch. & J., 26.03.2010. (typical "*congesta*"), PGB/3; **2011/81** Cao Bằng Province, Đèo Mã Phục (pass) 500 m towards Quảng Uyên, left side of the road, rock cavern, 610 m, 22°43.981'N, 106°20.333'E, leg. Hunyadi, A., 14.11.2011., HA/26, PGB/2; **2011/82** Lạng Sơn Province, Lũng Phầy (pass), Thất Khê N 13 km, 475 m, 22°20.363'N, 106°27.098'E, leg. Hunyadi, A., 15.11.2011., HA/8, PGB/1 (typical "*congesta*"); **2011/83** Cao Bằng Province, Đèo Lũng Phầy (pass) 2.5 km towards Đông Khê, right side of the road, 360 m, 22°21.654'N, 106°26.467'E, leg. Hunyadi, A., 15.11.2011., HA/17, PGB/2 (typical "*congesta*"); **2011/86** Cao Bằng Province, Quảng Uyên N, 206–207 cross, 300 m towards Hạ Lang, right side of the road, 445 m, 22°42.670'N, 106°27.260'E, leg. Hunyadi, A., 16.11.2011., HA/14, PGB/1; **2011/87** Cao Bằng Province, Quảng Uyên N, 206–207 cross, 430 m, 22°42.737'N, 106°27.223'E, leg. Hunyadi, A., 16.11.2011., HA/14, PGB/1 (anatomically examined, Figures 19, 28B, 29E, 30D, 32C, 35A–C); **2011/88** Cao Bằng Province, Quảng Uyên NW, 445 m, 22°42.562'N, 106°26.313'E, leg. Hunyadi, A., 16.11.2011., HA/6; **2011/89** Cao Bằng Province, Quảng Uyên W, Phi Hải-Đầu Tuyền cross, 500 m, 22°42.188'N, 106°26.358'E, leg. Hunyadi, A., 16.11.2011., HA/5; **2011/90** Cao Bằng Province, Quảng Uyên S 2 km towards Hồng Định, left side of the road, 470 m, 22°40.761'N, 106°26.746'E, leg. Hunyadi, A., 16.11.2011., HA/1; **2012/42** Cao Bằng Province, Quảng Uyên 10 km towards Cao Bằng, left side of the road, 620 m, 22°42.772'N, 106°21.582'E, leg. Hunyadi, A., 27.05.2012., HA/9; **2012/43** Cao Bằng Province, Pắc Rảo, Cảnh Tiên Commune cross, 300 m towards Trùng Khánh, right side of the road, 530 m, 22°49.385'N, 106°30.742'E, leg. Hunyadi, A., 28.05.2012., HA/13; **2012/44** Cao Bằng Province, southern edge of Pắc Rảo, Trùng Khánh 3 km towards Quảng Uyên, left side of the road, 570 m, 22°48.961'N, 106°30.533'E, leg. Hunyadi, A., 28.05.2012., HA/35; **2011/85** Cao Bằng Province, Cao Bằng 34.5 km towards Đông Khê, left side of the road, 500 m, 22°27.487'N, 106°25.047'E, leg. Hunyadi, A., 15.11.2011., HA/35, PGB/5 (typical "*congesta*"); **2011/84** Cao Bằng Province, Đông Khê 3 km towards Đèo Lũng Phầy (pass), right side of the road, 390 m, 22°24.223'N, 106°25.937'E, leg. Hunyadi, A., 15.11.2011., HA/10, PGB/2 (typical "*congesta*"); Cao Bằng Province, Hòa An District, Nguyễn Huệ Commune, small hill just outside of Khau Trang Village, 22°33.510'N, 106°10.294'E, leg. Naggs, F. et al., 22.06.2011., NHMUK/1 (see Figure 45A).

Diagnosis. Shell small to large, brownish (some Chinese populations are small and yellow, translucent), usually finely reticulated (resulting in a matt surface), umbilicus deep, dorsal side domed; apertural lip, callus and apertural fold very well-developed (Figure 9I). Parietal wall with two lamellae; the anterior one is usually connected to the lower plica; middle palatal plicae short, depressed Z-shaped, or almost vertical, sometimes connected to each other (Figures 13L–U).

Measurements (in mm): D = 13.5–14.1, D = 7–7.7 (n=2, 2011/84); D = 15.6–17, H = 7.7–10 (n=2, 2011/85); D = 19.9–20.3, H = 11–11.6 (n=2, 2011/81); D = 21.3, H = 12.1 (n=1, 2011/86).

Differential diagnosis. This species is most similar to *G. francoisi*. For comparisons, see under that species. *Gudeodiscus dautzenbergi* is larger, flatter, has wider umbilicus, a weaker apertural lip and the lower end of the anterior lamella is very much elongated anteriorly. *Gudeodiscus villedaryi* is also flatter and most populations have a keel around the umbilicus and an additional long plica below the parietal lamellae. *Gudeodiscus phlyarius* is usually flatter, has a wider umbilicus, slimmer peristome and lower callus. Most specimens of *G. phlyarius* have separated anterior lamella and lower plica, whereas these are always connected in *G. giardi giardi*. Typical *Plectopylis verecunda* shells (synonym of *G. phlyarius*) also have an elevated spire, but their shell shape is rather conical, whereas it is usually domed (rounded) in *G. giardi*.

Intraspecific diversity. Two subspecies of *Gudeodiscus giardi* were described from China (see Páll-Gergely and Hunyadi 2013). The populations assigned to the nominotypical subspecies show larger variability in China in terms of shell size, colour and shape, than in Vietnam. In Vietnam *G. giardi giardi* is moderately variable. Most variability is observable in the formation of the parietal plicae and lamellae (see Remarks and Figures 13L–U).

Description of the genitalia. One specimen was anatomically examined (see also Remarks). Locality: Cao Bằng Province, Quảng Uyên N, 206–207 cross, 430 m, 22°42.737'N, 106°27.223'E, leg. Hunyadi, A., 16.11.2011. (Figure 28B, 29E, 30D, 32C).

Penis very short, almost ball-like; penis wall conspicuously thickened, its inner surface is characterized by transversal lines at the proximal part and longitudinal pockets in the distal part, arranged in a straight row (Figure 28B); there are some calcareous, claw-like objects in the pockets; the claws have a wide, rounded basal part which is found within the pockets, and the short, hook-like part hangs out of the pockets; the base had a granulated surface, probably to provide a better attachment to wall of the pockets, whereas the tip was smooth (Figure 30D); epiphallus C-shaped, longer than the penis; its inner wall with three longitudinal parallel folds (Figure 29E); penis and epiphallus connected with weak membrane; penial caecum approximately as long as the penis; it has low tubercles on the inner wall and small calcareous rounded granules on each tubercle; retractor muscle attaches on the distal part of the penial caecum; it is longer and wider than the caecum; vas deferens convoluted near the vagina. Vagina very thick and long, it is attached to the body wall with several thin ligaments; one side of the vaginal bulb with very much thickened wall, the other side with thin, almost translucent wall, internally with fine, irregular, reticulated sculpture; inner wall of the distal portion of the vagina with well-developed, rather irregular transversal folds (Figure 32C); gametolytic sac and diverticulum slender, they are nearly the same length.

Radula. See Table 6 and Figures 35A–C.

Distribution (see Figure 42): Newly-collected material was examined from Cao Bằng Province and the northern part of Lạng Sơn Province. The localities of "Col de Nuages" and "Halong Bay" are probably erroneous. This species is also known from the western part of Guangxi, China (Páll-Gergely and Hunyadi 2013).

Remarks. *Plectopylis congesta* Gude, 1899 was described without exact locality data. Some shells from populations in southern Cao Bằng and northern Lạng Sơn prefectures (Vn10-69; 2011/84, 2011/83, 2011/82, 2011/85) resemble the holotype of *P. congesta* on the basis of relatively weak peristome and callus, weak (low) posterior lamella and the anterior lamella which is fused to the upper parietal plica. These populations however, falls within the morphological range of the very variable *Gudeodiscus giardi giardi*, therefore *P. congesta* is here synonymised with *G. giardi giardi*.

The genital anatomy of a Chinese specimen of *Gudeodiscus giardi giardi* was described by Páll-Gergely and Asami (2014). The only notable difference between the Chinese and Vietnamese specimens is the much longer penis in the Chinese individual. It seems that the long, slender, proximal portion of the penis visible in the Chinese specimen is entirely missing in the Vietnamese one.

***Gudeodiscus* (*Gudeodiscus*?) *hemmeni* Páll-Gergely & Hunyadi, sp. n.**

http://zoobank.org/5A98BC18-CF82-4C2F-BCE4-DCCA8DBBED3B
Figures 2C–D, 9F, 11G–J

Type material. 2012/61 Sơn La Province, Hà Nội 156 km towards Mộc Châu, left side of the road nr. 6, rocky wall, 1110 m, 20°45.993'N, 104°53.868'E, leg. Hunyadi, A., 06.06.2012., holotype HNHM 97458 (Figure 2C), HA/11 paratypes+4jb (not paratype), PGB/3 paratypes; **2012/62** Sơn La Province, Hà Nội 156 km towards Mộc Châu, right side of the road nr. 6, rocky wall, 1110 m, 20°46.085'N, 104°53.888'E, leg. Hunyadi, A., 06.06.2012., HA/13 paratypes+2jb (not paratypes), PGB/1; **Vn12-104** Sơn La Province, right side off road Mộc Châu to Sơn La, 20°52.567'N, 104°35.310'E, leg. Hemmen, Ch., 02.10.2012., HE/1; **Vn10-103A** Hòa Bình Province, ca. km 156 old road Hà Nội to Sơn La (right side off road), 20°46.000'N, 104°53.885'E, leg. Hemmen, Ch. & J., 15.10.2010., HE/1 (Figure 2D); **Vn10-76A** Sơn La Province, ca. 32 km from Mộc Châu to Hà Nội (old road), 20°47.351'N, 104°50.063'E, leg. Hemmen, Ch. & J., 02.04.2010., HE/1.

Diagnosis. Shell small, with slightly elevated spire, characteristically shaped aperture having wide upper sinulus and small apertural fold (Figure 9F); parietal wall with two lamellae and horizontal plicae above and below; palatal plicae depressed Z-shaped; free from each other, or connected to each other with a ridge (Figures 11G–J).

Description. Shell very small to small, light brown to chocolate brown, with slightly elevated spire, consists of 5.25–5.5 whorls; suture relatively shallow, especially at the first 3–4 whorls; protoconch (2.25–2.5 whorls) glossy, very finely, regularly ribbed, but the ribs are sometimes hardly visible, they are more prominent at the upper part of the whorls, close to the suture; teleoconch without notable spiral lines, very finely regularly ribbed; sculpture strength equal on ventral and dorsal side; umbilicus narrow and deep; aperture with widened upper part (sinulus), apertural lip whitish, thin, slightly expanded but not reflexed; apertural denticle (fold) always present, very small, free from the callus or connected to it.

Two specimens were opened. Parietal side with a stronger anterior lamella with anteriorly widened lower part, and a slimmer posterior lamella; shorter upper and longer lower horizontal plicae free from the anterior lamella, the lower one a bit extends beyond the anterior lamella in the anterior direction. Palatal side with six plicae; first and last are straight, the others are depressed Z-shaped and are connected with a ridge.

Measurements (in mm): D = 9.5–10.1, H = 4.3–5.2 (n=5, belonging to different populations).

Differential diagnosis. *Gudeodiscus hemmeni* sp. n. differs from most *G. phlyarius* populations by the smaller shell, shorter denticle (fold) in the aperture, thinner apertural lip, the wider and reflexed apertural rim, the wide upper sinus of the aperture, lack of spiral lines in the sculpture and narrower umbilicus. *Gudeodiscus anceyi* is usually smaller, has a longer apertural fold, prominent spiral sculpture, a weaker callus and differently shaped aperture.

In all localities, *Gudeodiscus hemmeni* sp. n. lives sympatrically with *G. messageri raheemi* ssp. n., which is much larger, lacks the apertural fold, and usually has an anterior lamella which is dissolved into small denticles.

Intraspecific diversity. Low; shell characters are stable, although only a few shells are known.

Etymology. The new species is dedicated to Jens Hemmen (1944–2012), malacologist and much-valued friend, who contributed to our revision by providing shell and ethanol-preserved material.

Type locality. Sơn La Province, Hà Nội 156 km towards Mộc Châu, left side of the road nr. 6, rocky wall, 1110 m, 20°45.993'N, 104°53.868'E.

Distribution (see Figure 43). The new species is known from few locations in south-eastern Sơn La province.

Gudeodiscus (*Gudeodiscus*?) *infralevis* (Gude, 1908)

Figures 3D–E, 15A–D

1908 *Plectopylis infralevis* Gude, Journal de Conchyliologie, 55: 345, 350, 352–353., Figs 3a–e, Plate 7, Figs 4–6. ["Quang Huyen"].
1908 *Plectopylis soror* Gude, **syn. n.**, Journal de Conchyliologie, 55: 355–357., Figs 5a–e, Plate 7, Figs 10–12. ["Quang Huyen"].
2013 *Gudeodiscus infralevis*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.
2013 *Gudeodiscus soror*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

Types examined. Tonkin, Quang-Huyen, leg. Mansuy, MNHN 24604 (holotype of *infralevis*, Figure 3D); Tonkin, Quang-Huyen, leg. Mansuy, MNHN 24585 (holotype of *soror*, Figure 3E).

Diagnosis. Shell small, solid, discoid, with elevated spire, relatively deep umbilicus; relatively thin apertural lip and rather parallel, thick, straight palatal plicae. See also under remarks.

Measurements (in mm): D = 13.9, D = 6.7 (*soror* holotype); D = 13.5, H = 6.6 (*infralevis* holotype).

Differential diagnosis. Our knowledge on the intraspecific variety of the species is very limited (see Remarks). It seems that the thick, rather horizontal palatal plicae, the strong basal sculpture and the elevated spire distinguishes the species from the similar species (*Gudeodiscus eroessi*, *G. multispira*, *G. soosi*, *G. yunnanensis*, *G. cyrtochilus* and *G. fischeri*). The shell and aperture shape suggest that the closest relatives are *G. fischeri* and *G. suprafilaris* (see comparisons under those species).

Intraspecific diversity. *Plectopylis infralevis* and *P. soror* are considered as conspecific (see Remarks). Only the holotypes of these taxa are known, therefore our knowledge on the intraspecific variability is limited.

Distribution. The type specimens of *Plectopylis infralevis* and *P. soror* (synonym of *infralevis*) were collected in Quang Huyen (Quảng Uyên) (see Figure 39).

Remarks. Only the holotypes of *Plectopylis infralevis* and *P. soror* are known. The notable differences between these two shells are the stronger sculpture, slightly shouldered body whorl and small apertural fold in *soror*. Additionally, there are three lamellae in *infralevis* versus only one in *soror*. The three vertical lamellae in the holotype of *infralevis* is possibly the result of abnormal development. No other species of Plectopylidae has three lamellae. Similar abnormal shells have been reported in *Gudeodiscus* *giardi* (see Gude 1908). Consequently, we do not know what the characteristic type of parietal lamellae in this species is (=one or two). The differences between the two specimens suggest only intraspecific variance. Unfortunately we have no freshly-collected material of these two forms, but because of the high similarity between the two holotypes and same type locality we here synonymise *soror* with *infralevis*. These two names were published in the same paper (Gude 1908), but *infralevis* was described earlier in terms of page numbers.

Gudeodiscus (*Gudeodiscus*) *messageri* (Gude, 1909)

Diagnosis. Shell small to medium-sized, with slightly elevated spire, dorsal surface somewhat domed; aperture almost circular, apertural fold missing; callus rather blunt and only slightly curved. Parietal wall with two lamellae (the anterior lamella may be dissolved into small denticles); lower parietal plica free or connected to the anterior lamella; palatal plicae oblique, or depressed Z-shaped, usually in contact with each other.

Differential diagnosis. See under the two subspecies.

Gudeodiscus (*Gudeodiscus*) *messageri messageri* (Gude, 1909)

Figures 5F–G, 9E, 12N–Q

1909 *Plectopylis messageri* Gude, Proceedings of the Malacological Society of London, 8: 214–215., Plate 9, Figs 4, 4a–b [“Moung-Hum”, “Nat-Son, Pac-Kha, and Trinh-Tuong”].

2013 *Gudeodiscus messageri*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 8.

Types examined. Tonkin, Muong-Hum, leg. Messager, NHMUK 1922.8.29.53 (holotype of *Plectopylis messageri*, Figure 5F), Tonkin, Nat-Son, leg. Messager, NHMUK 1922.8.29.54 (holotype of *messageri* var. *minor*, Figure 5G).

Museum material examined. Tonkin, coll. Dosch ex Rolle ex Messager, SMF 172088/4; Tonkin, coll. Dosch ex Rolle, SMF 172076/2; Tonkin, Trinh-Tuong, coll. Dosch ex Rolle, SMF 172086/4; Tonkin, Drinch-Tuom (Trinh-Thuong?), coll. Jaeckel ex Messager, SMF 207675/3; Tonkin, alw. Müller, coll. Kaltenbach, SMF 294867/2; Tonkin, Gia-Phu, coll. Dosch ex Rolle, SMF 172089/4; Tonkin, Muong-Bo, coll. Dosch ex Rolle, SMF 172087/4; Tonkin, Muong-Kong, coll. Pfeiffer, K. L. ex Naschloss (?) ex Rolle, January 1938, SMF 102820/1; Tonkin, coll. Dosch ex Rolle ex Messager, SMF 182088/4; Tonkin, Ba-Nat (?), NHMSB 131/200, 122812-122813/2; Pakhé, leg. Messager, MNHN-IM-2012-2129/9; Muong-Hum, leg. Messager, MNHN-IM-2012-2134/15; Nat-Son, Trinh-Thuong, leg. Messager, MNHN-IM-2012-2136/16 („var. *minor*“); Muong-Kong, leg. Messager, MNHN-IM-2012-2137/4; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2142/2+4jb;

Muong-Hum, leg. Messager, MNHN-IM-2012-2131/5; Muong-Hum, leg. Messager, MNHN-IM-2012-2143/3; Muong-Hum, leg. Messager, MNHN-IM-2012-2145/74; Pakhé, leg. Messager, MNHN-IM-2012-2149/1; Pac-Kha (Pakhé), leg. Messager, MNHN-IM-2012-2151/10; Nat-Son, leg. Messager, MNHN-IM-2012-2154/6; Muong-Kong, leg. Messager, MNHN-IM-2012-2159/1; Nat-Son, leg. Messager, MNHN-IM-2012-2162/29; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2163/20; Nat-Son, leg. Messager, MNHN-IM-2012-2165/8+25jb; Bac-Kan, leg. Messager, MNHN-IM-2012-2166/6; Bac-Kan, leg. Messager, MNHN-IM-2012-2172/4; Muong-Hum, leg. Messager, MNHN-IM-2012-2173/3; Muong-Hum, leg. Messager, MNHN-IM-2012-2183/4; Pakhé, leg. Messager, MNHN-IM-2012-2184/1; Long-Ping, leg. Messager, MNHN-IM-2012-2186/8; Muong-Hum, leg. Messager, MNHN-IM-2012-2188/8; Bac-Kan, leg. Messager, MNHN-IM-2012-2194/3; Muong-Hum, leg. Messager, MNHN-IM-2012-2196/4; Nat-Son, leg. Messager, MNHN-IM-2012-2198/2; Nat-Son, leg. Messager, MNHN-IM-2012-2199/2; Tonkin, leg. Messager, MNHN-IM-2012-2202/1; Trinh Thuong, leg. Messager, MNHN-IM-2012-2205/12; Muong-Kong, leg. Messager, MNHN-IM-2012-2479/1; Bac-Kan, leg. Messager, MNHN-IM-2012-2475/10; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2472/16; Cao-Bang, leg. Messager, MNHN-IM-2012-2471/1; Tonkin, Pakhé, leg. Messager, MNHN-IM-2012-2458/7; Long-Ping, leg. Messager, MNHN-IM-2012-2457/23; label not readable, leg. Messager, MNHN-IM-2012-2449/2; Bac-Kan, leg. Messager, MNHN-IM-2012-2403/1; Trinh-Thuong, coll. Levazzari, 1929, MNHN-IM-2012-2408/9; Tonkin, coll. Staadt, 1969, MNHN-IM-2012-2411/3; Nat-Son, coll. Letellier, 1949, MNHN-IM-2012-2414/2; Pac-Kha, coll. Letellier, 1949, MNHN-IM-2012-2415/2; Gia-Phu, MNHN-IM-2012-2418/3; Trinh-Thuong, coll. Lavezzari, 1929, MNHN-IM-2012-2419/10; Tonkin, leg. Messager, MNHN-IM-2012-2425/3; Gia-Phu, leg. Messager, MNHN-IM-2012-2215/33; Muong-Hum, leg. Messager, MNHN-IM-2012-2216/3; Long-Ping, leg. Messager, MNHN-IM-2012-2217/9; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2219/12; Col de Nuages, leg. Messager, MNHN-IM-2012-2221/1; Trinh Tuong, leg. Messager, MNHN-IM-2012-2223/2; Tonkin, leg. Messager, MNHN-IM-2012-2225/4; Tonkin, leg. Messager, MNHN-IM-2012-2230/1; Long-Phai, leg. Messager, 1901, MNHN-IM-2012-2237/2; Muang-Kong, leg. Messager, MNHN-IM-2012-2242/3; Nat-Son, coll. Staadt, 1969, MNHN-IM-2012-2282/1; Tonkin, leg. M. Balansa, 1889 July, MNHN-IM-2012-2296/10; Pakhé, leg. Messager, MNHN-IM-2012-2339/1; Bac-Kan, leg. Messager, MNHN-IM-2012-2315/1; Gia-Phu, leg. Messager, MNHN-IM-2012-2364/2; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2379/1; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2394/1; Tonkin, Pac-Kha, NHMUK1916.3.16.15/1; Tonkin, Pac-Kha, coll. Kennard, A.S. ex auct. (Gude), NHMUK 20130620.2/1; Tonkin, Muong-Hum, coll. Biggs, H.E.J. ex Gygngell, 1930, Acc. no. 2258, NHMUK 20130626/2; Tonkin, Gia-Phu, coll. Kennard, A.S. ex auct. (Gude), NHMUK 20130627/2; Tonkin, Muong-Kong, coll. Salisbury ex Beddome, NHMUK 20130628/2; Tonkin, Muong-Kong, 31/3/09, NHMUK 20130629/3; Tonkin, Muong-Hum, 5/1/09, NHMUK 20130630/3; Tonkin, Pac-Kha, 3/11/08, NHMUK 20130631/2 ("var. *minor*"); Tonkin, 5/1/09, NHMUK 20130632/3; Tonkin, Muong-Hum, coll. Preston, NHMUK 20130633/2; Tonkin, Muong-Bo, 3/11/08, NHMUK 20130634/2 ("var. *major*"); Tonkin, That-Khé, coll. Salisbury ex Beddome, NHMUK 20130635/1; Tonkin, Muong-Hum, coll. Kennard, NHMUK 20130636/1; Tonkin, Muong-Hum, NHMUK 1909.3.17.29–31/3; Tonkin, Muong-Hum, NHMUK 1916.3.16.16-18/3; Tonkin, Pac-Kha, NHMUK 1909.3.17.32–34/3 ("var. *minor*"); Tonkin, Pac-Kha, NHMUK 1909.3.17.24–25/2; Tonkin, Muong-Bo, NHMUK 1909.3.17.35–36/2 ("var. *major*"); Tonkin, Gia-Phee, coll. Rušnov ex Rolle ex Messager, NHMW 92576/1; Tonkin, Trisch-Tuong, coll. Edlauer ex Werner, NHMW 75000/E/7983/2; Tonkin, Muong-Hum, coll. Oberwimmer ex Wagner ex Messager, NHMW 92573/2; Tonkin, Bac-Kan, coll. Oberwimmer, NHMW 71640/O/14028/1; Tonkin, Long-Ping, 3000 m, coll. Oberwimmer ex Wagner ex Messager, NHMW 92572/1; Tonkin, Muong Hum, coll. Rosen ex Messager, NHMW 71640/O/9476/2; Tonkin, Trinh-Tua (?), coll. Rolle, NHMW 92574/2; Tonkin, Ban-Tao, coll. Rušnov ex Blume, NHMW 92575/1; Tonkin, Muong Kong, NHMW 71640/O/46293/2; Tonkin, Nat-Son, coll. Rosen ex Messager, NHMW 71640/O/9477/1; Tonkin, Trisch Tuong, coll. Rušnov ex Rolle ex Messager, NHMW 92578/2; Tonkin, Ban-Lao, coll. Rolle, NHMW 92577/1; Tonkin, Bac-Kan, coll. Oberwimmer, NHMW 92567; Tonkin, Bac-Kan, coll. Oberwimmer, NHMW 103353/1; Tonkin, Nat-Son, coll. Rušnov ex Messager, NHMW 103355/1; Vietnam/132, Lao Cai Province, Cox-Xan, 400 m, leg. Topál & Matskási, 27.11.1971., VA/10.

Diagnosis. At least one shell was opened of every larger samples. Anterior lamella normal (not dissolved into small denticles); lower parietal plica does not extend beyond the anterior lamella in the anterior direction (Figures 12N–Q).

Measurements (in mm). D = 12.75–18.5 (according to the original description).

Differential diagnosis. *Gudeodiscus messageri messageri* inhabits northern Vietnam and in many museum samples it is mixed with *Plectopylis gouldingi* or *Plectopylis fallax* (synonyms of *G. phlyarius*). These two forms have flat shells with a sharp and angled callus, and sometimes with an apertural denticle. Also, the aperture of *G. messageri* is rather rounded, whereas it is rather elongated in those populations of *G. phlyarius* (Figures 9D: *phlyarius*, Figure 9E: *messageri*). This allows *G. messageri* and *G. phlyarius* to be distinguished without breaking the shell. The lower parietal plica, which does not extend beyond the anterior lamella in the anterior direction, is characteristic of *G. messageri messageri* (see also Remarks), but almost always extends in "*P. fallax*" and "*P. gouldingi*". "*Plectopylis verecunda*" (synonym of *G. phlyarius*) and typical *G. phlyarius* always have a strong apertural fold. Moreover, the lower parietal plica of the latter usually extends beyond the anterior lamella in the anterior direction. For comparison with *G. messageri raheemi* ssp. n., see there.

Intrasubpecific diversity. Low; the shell size, and the relationship between the lower parietal plica and the anterior lamella show some variability (see remarks). The shell and aperture shape are stable characters.

Distribution (see Figure 43): Only museum material was available for study, which suggested that this species is located along the Chinese (Yunnan) border.

Remarks. In one sample (MNHN-IM-2012-2215) a specimen had longer lower plica which extended beyond the anterior lamella in the anterior direction.

***Gudeodiscus* (*Gudeodiscus*) *messageri raheemi* Páll-Gergely & Hunyadi, ssp. n.**
Figures 5D, 5E, 10A, 12R–V, 20, 28E, 29F–G, 31B, 35D–F

Type material. Thanh Hoa Province, Cam Thuy District, Fish Stream, leg. Naggs, F. & Hao, L.V., 13.05.2008., NHMUK 20110370.1–3 (holotype and two paratype); **MAA10** Ninh Bình Province, Cúc Phương Nat. Park, path to fairy cave, approximate GPS position: 20°21'N, 105°54'E, leg. Vermeulen, J., coll. Maassen, W.J.M., 10.10.1998., PGB/1 paratype, WM/3 paratypes; **MAA1** Thanh Hóa Province, Pù Luông Nat. Park, NW corner of park near Hang village, limestone area near village, 20°31.84'N, 105°04.76'E, coll. Maassen, W.J.M., 19.09.2003., PGB/1 paratype, WM/3 paratypes; **MAA9** Thanh Hóa Province, Pù Luông Nat. Park, limestone hill opposite village Naca, 20°26.86'N, 105°11.57'E, coll. Maassen, W.J.M., 20.09.2003. WM/2 paratypes; **Vn10-76A** Sơn La Province, ca. 32 km from Mộc Châu to Hà Nội (old road), 20°47.351'N, 104°50.063'E, leg. Hemmen, Ch. & J., 07.10.2010., HE/1 paratype, PGB/2 paratypes; same locality data, leg. Hemmen, Ch., 01.10.2012., HE/1 paratype; **Vn10-103** Hòa Bình Province, ca. km 156 old road Hà Nội to Sơn La (right side off road), 20°46.000'N, 104°53.885'E, leg. Hemmen, Ch. & J., 15.10.2010., HE/2 paratypes, PGB/1 paratype, and one paratype in ethanol (anatomically examined, Figure 20); **20080509C** Nghệ An Province, Pù Mát Nat. Park, Con Cuông Dist., Lục Dạ Commune, Tân Hợp Village, ca 90 m, 18°57.80201'N, 104°54.67774'E, leg. Ohara, K., 09.05.2008., OK/5 paratypes, PGB/2 paratypes; **20071118A** Thanh Hóa Province, Trang Village, Bá Thước. (Bee Cave Mt.), Lân Sa Commune, ca 40 m, 20°19.92147'N, 105°12.49178'E, leg. Ohara, K., 2007.11.18., PGB/1 paratype; **20071118B** Thanh Hóa Province, Cây Đăng Cave, Lương Ngọc, Cẩm Lương C., (GPS not recorded), leg. Ohara, K., 18.11.2007., PGB/1 paratype; **20071116C** Ninh Bình Province, Cúc Phương Nat. Park, Cave of Prehistoric Man, ca 145 m, 20°15.53843'N, 105°42.38950'E, leg. Ohara, K., 16.11.2007., PGB/2 paratypes; **Vn10-104B** Sơn La Province, right side off road Mộc Châu to Sơn La, 20°52.567'N, 104°35.310'E, leg. Hemmen, Ch., 02.10.2012., HE/7 paratypes; same data, leg. Hemmen, Ch. & J., 08.10.2010., PGB/2 paratypes; same data, leg. Hemmen, Ch. & J., 14.10.2011., HE/17 paratypes; **2011/106** Ninh Bình Province, Cúc Phương Nat. Park, main entrance, 700 m towards Bống Village, 155 m, 20°15.231'N, 105°42.639', leg. Hunyadi, A., 22.11.2011., HA/12 paratypes +1jb (not paratype), PGB/2 paratypes; **2011/108** Ninh Bình Province, Cúc Phương Nat. Park, Động Người Xưa (=Prehistoric Men Cave), around the cave, 20°17.615'N, 105°40.115'E, leg. Hunyadi, A., 23.11.2011., HA/6 paratypes; **2011/113** Thanh Hóa Province, Cẩm Lương, Động Cây Đăng (cave), around the cave, 60 m, 20°15.128'N, 105°23.404'E, leg. Hunyadi, A., 25.11.2011., HA/6 paratypes +5jb (not paratypes); **2012/10** Nghệ An Province, Con Cuông 20 km towards Anh Sơn, right side of the road, 40 m, 18°58.302'N, 105°00.796'E, leg. Hunyadi, A., 15.05.2012., HA/7 paratypes +11jb (not paratypes); **2012/60** Sơn La Province, Mộc Châu 5 km towards Sơn La, right side of the road nr. 6, 755 m, 20°52.551'N, 104°35.318'E, leg. Hunyadi, A., 06.06.2012., HA/6 paratypes +16jb (not paratypes), PGB/1 paratypes; **2012/61** Sơn La Province, Hà Nội 156 km towards Mộc Châu, left side of the road nr. 6, 1100 m, 20°45.993'N, 104°53.868'E, leg. Hunyadi, A., 06.06.2012., HA/3 paratypes +2jb (not paratypes); **2012/62** Sơn La Province, Hà Nội 156 km towards Mộc Châu, right side of the road nr. 6., rocky wall, 1110 m, 20°46.085'N, 104°53.888'E, leg. Hunyadi, A., 06.06.2012., HA/5 paratypes+2jb (not paratypes), PGB/1 paratype; **Vn12-80A** Thanh Hóa Province, Cẩm Thạch, opp. Cẩm Lương Fishstream (W Cẩm Thủy), 20°15.234'N, 105°23.530'E, leg. Hemmen, Ch., 08.10.2012., HE/5 paratypes; same data, leg. Hemmen, Ch. & J., 04.04.2010., HE/2 paratypes; **Vn11-215** Sơn La Province, ca. 34 km from Mộc Châu to Mai Châu, 20°45.219'N, 104°54.458'E, leg. Hemmen, Ch. & J., 15.10.2011., HE/1 paratype; **Vn11-230** Nghệ An Province, ca. 1.2 km left off rd 48, ca 23 km from Thái Hòa to Qùy Châu, 19°24.363'N, 105°26.521'E, leg. Hemmen, Ch. & J., 22.10.2011., HE/1 paratype; **Vn12-268** Thanh Hóa Province, km 585 on road 15 Yến Cát to Ngọc Lặc 1 km right off road 15, 19°45.589'N, 105°25.521'E, leg. Hemmen, Ch. & J., 14.04.2012., HE/3 paratype; **20080510A** Nghệ An Province, Pù Huống Nature Reserve, Con Coung District, Anh Son, Hoi Son, ca 30 m, 18°57.11872'N, 105°02.63029'E, leg. Ohara, K, Okubo, K & Otani, J. U., Sang, 10.05.2008., 1 paratype in ethanol, anatomically examined.

Diagnosis. Anterior lamella normal or dissolved into small denticles, if normal, the lower plica extends beyond the anterior lamella in the anterior direction (Figures 12R–V).

Description. Shell medium in size, light to dark brown or dark yellowish, sometimes almost flat but usually with slightly elevated spire, consists of 6.25–6.75 whorls; suture relatively shallow; protoconch (2.5–2.75 whorls) glossy, very finely, regularly ribbed; teleoconch very finely, rather irregularly ribbed, spiral lines visible mainly at the dorsal side where sometimes they are as strong as the ribs (resulting in a reticulated surface), in some specimens however hardly any spiral lines are visible; sculpture weaker on the ventral side but within the umbilicus are as strong as on the dorsal side; umbilicus relatively narrow and deep; aperture wide with whitish or light brown, thickened and reflexed apertural rim; callus slightly S-shaped, well-developed, with upper and with or without lower canal between the ends of callus and the apertural lip; apertural fold always missing.

More than ten specimens were opened belonging to different populations. Parietal side with two lamellae and upper and lower horizontal plicae above and below the anterior lamella; the lower plica usually extends beyond the anterior lamella in the anterior direction; in some populations the anterior lamella (or only the upper part of the lamella) is dissolved into several denticles. Palatal wall with six plicae; first and last are short and relatively straight, the four middle plicae are usually depressed Z-shaped and in many cases connected to each other with a ridge.

Measurements (in mm). D = 12.9–14.4, H = 6.2–7.5 (n=3, Vn10-76); D = 14.2–14.4, H = 6.8–7.9 (n=3, 20071116C); D = 12.1, H = 6 (n=1, Vn11-230); D = 16–17.9, H = 7.3–7.9 (n=3, Vn11-104).

Differential diagnosis. The lower parietal plica extends beyond the anterior lamella in the anterior direction, which is extremely rarely the case in the nominotypical subspecies. The anterior lamella was dissolved into small denticles in many samples, which has never been observed in the nominotypical subspecies (Figures 12N–Q: *messageri*, 12R–V: *raheemi* ssp. n.). The umbilicus of the new subspecies is narrower, it has more rounded whorls and a sharper, more angled callus, than in most samples of *Gudeodiscus messageri messageri*.

Gudeodiscus messageri raheemi ssp. n. lives sympatrically with an atypical form of *G. phlyarius* in Ninh Bình Province (see under *G. phlyarius*). *Gudeodiscus phlyarius* is flat and has an apertural fold, whereas *G. messageri raheemi* ssp. n. has somewhat elevated spire and always lacks the apertural fold. See also under *G. hemmeni* sp. n.

Intrasubspecific diversity. Relatively variable; the colour, spire height, size and morphology of the palatal and parietal lamellae and plicae show considerable variability (see Table 8).

Description of the genitalia. Two specimens were anatomically examined. Both specimens had embryos developing in their uterus. Localities: "Specimen1", Hòa Bình Province, ca. km 156 old road Hà Nội to Sơn La (right side off road), 20°46.000'N, 104°53.885'E, leg. Hemmen, Ch. & J., 15.10.2010. (with 3 embryos, Figures 20, 29F, 31B, 35D–F); "Specimen2", Nghệ An Province, Pù Huống Nature Reserve, Con Coung District, Anh Son, Hoi Son, ca 30 m, 18°57.11872'N, 105°02.63029'E, leg. Ohara, K, Okubo, K & Otani, J. U., Sang, 10.05.2008. (Figures 28E, 29G).

Penis relatively short and slim, attached to the slightly shorter epiphallus by weak fibres; penis internally with longitudinal folds; the folds are more elevated in the distal part of the penis and they from characteristic "pockets" (Figure 28E); the pockets are arranged in two rows, the upper row (closer the distal end of the penis) is slightly curved on the opened penial wall, but the lower row follows a a wavy line with two peaks; epiphallus have longitudinal folds on the inner wall; penial caecum long; "Specimen1" had two times longer caecum than "Specimen2"; internally with small hollows arranged in longitudinal lines (Figure 29F); "Specimen2" had a few elongated and globular calcareous granules within the hollows (Figure 29G); retractor muscle very long and slim, attaches on the distal end of the penial caecum; vas deferens very long. Vagina extremely long, cylindrical in "Specimen1" and with well-developed vaginal bulb in "Specimen2"; inner wall of the vagina with 6–8 low, parallel or converging folds (Figure 31B); gametolytic sac and diverticulum of the same length, both relatively slim, although the gametolytic sac is a bit swollen.

Radula. See Table 6 and Figures 35D–F.

Etymology. The new subspecies is dedicated to and named after our colleague and much-valued friend, Dinarzarde Raheem.

Type locality. Thanh Hoa Province, Cam Thuy District.

Distribution (see Figure 43). The new subspecies is known from several localities in Ninh Bình, Thanh Hóa, Sơn La, Hòa Bình and Nghệ An provinces.

Table 8. Diversity of shell characters within *Gudeodiscus* (*Gudeodiscus*) *messageri raheemi* ssp. n.

code	shell colour	spire	anterior lamella	lower plica	shells opened
20071118B	yellow	very slightly elevated	dissolved	reaches lamella	1
2012/62	dark yellow	slightly elevated	normal or dissolved	exctends lamella	2
20080509C	yellowish-corneous	slightly elevated	normal	exctends lamella	1
2007.11.16C= 2011/106	dark yellow	very slightly elevated	dissolved	exctends lamella	2
Vn12-104= Vn10-103, 2012/60	light or dark brown	slightly elevated	normal or dissolved	reaches or exctends lamella	4
20071118A	dark brown	slightly elevated	dissolved	exctends lamella	1
Vn10-76	dark brown	slightly elevated	dissolved or with buttresses	reaches or almost reaches lamella	1
MAA1	yellowish-corneous	slightly elevated	dissolved	reaches lamella	1

***Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887)**

Figures 4A–F, 5A–C, 9C–D, 10C–F, 11K–X, 12A–M, 21–22, 28A, 28C, 31C, 35J–L

1887a *Plectopylis phlyaria* Mabille, Molluscorum Tonkinorum diagnoses: 6. [type locality not specified].

1887b *Plectopylis phlyaria.* Mabille, Bulletin de le Société Malacologique de France, 4: 100–101., Plate 2, Figs 1–3.

1893 *Plectopylis phlyaria*, — Pilsbry, Manual of Conchology..., 2(8): 158, Plate 43, Figs 40–42.

1897b *Plectopylis phlyaria*, — Gude, Science Gossip, 4: 139., Figs 61a–b. [“Tonkin”].

1899c *Plectopylis* (*Endoplon*) *phlyaria*, — Gude, Science Gossip, 4: 148.

1899d *Plectopylis* (*Endoplon*) *phlyaria*, — Gude, Science Gossip, 6: 175.

1901c *Plectopylis* (*Endoplon*) *phylaria*, — Gude, Journal of Malacology, 8: 113–115., Figs 3a–f. [“Than Moi”].

1901c *Plectopylis* (*Endoplon*) *moellendorffi* Gude, Journal of Malacology, 8: 115–116., Figs 4a–f. [“Than-Moi”].

1909 *Plectopylis gouldingi* Gude, **syn. n.**, Proceedings of the Malacological Society of London, 8: 215, 217., Plate 9, Figs 1, 1a–b. [“Nat-Son”].

1909 *Plectopylis verecunda* Gude, **syn. n.**, Proceedings of the Malacological Society of London, 8: 215, Plate 9, Figs 3, 3a–b. [“Phony-Tho”].

1909 *Plectopylis fallax* Gude, **syn. n.**, Proceedings of the Malacological Society of London, 8: 217, Plate 9, Figs 6, 6a–b. [“Muong-Bo”].

1909 *Plectopylis anterides* Gude, **syn. n.**, Proceedings of the Malacological Society of London, 8: 216, Plate 9, Figs 2, 2a–b. [“Pac-Kha”].

2013 *Gudeodiscus phlyarius phlyarius* (and *Plectopylis moellendorffi* is synonym), — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 25–28., Figs 31, 61a–b, 63–65, 75 (map) 77a–b, 112–114.
2013 *Gudeodiscus fallax*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.
2013 *Gudeodiscus gouldingi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.
2013 *Gudeodiscus verecundus*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.
2013 *Gudeodiscus phlyarius werneri* Páll-Gergely in Páll-Gergely & Hunyadi, **syn. n.**, Archiv für Molluskenkunde 142 (1): 13: Figs 32, 28–29, 34: Figs 76a–d.

Types examined. Tonkin, Muong-Bo, leg. Messager, NHMUK 1922.8.29.58 (holotype of *fallax*, Figure 5C); Tonkin, Nat-Son, leg. Messager, NHMUK 1922.8.29.56 (holotype of *gouldingi*, Figure 4E); Tonkin, Pac-Kha, NHMUK 1922.8.29.57 (holotype of *anterides*, Figure 4F); Tonkin, MNHN 24581 (2 syntypes of *phlyaria*, Figure 4A); Tonkin, Than-Moi, collection Möllendorff ex Fruhstorfer, SMF 150125a (lectotype of *moellendorffi*, Figure 4B); Tonkin, Than-Moi, collection Möllendorff ex Fruhstorfer, SMF 150125b (paralectotype of *moellendorffi*); Tonkin, Phony-Tho, leg. Messager, NHMUK 1922.8.29.55 (holotype of *verecunda*, Figure 5B).

Museum material examined. *fallax*-like shells. Tonkin, région de Lao Kay, coll. Dosch ex Rolle, SMF 172081/4; Tonkin, Muong-Bo, coll. Dosch ex Rolle, SMF 172077/2; Tonkin, Muong-Kong, coll. Dosch ex Rolle, SMF 172080/4; Muong-Hum, leg. Messager, MNHN-IM-2012-2130/1; Pakhé, leg. Messager, MNHN-IM-2012-2132/19; Pakhé, leg. Messager, MNHN-IM-2012-2135/6; Muong-Kong, leg. Messager, MNHN-IM-2012-2138/2; Muong-Kong, leg. Messager, MNHN-IM-2012-2140/3; Muong-Hum, leg. Messager, MNHN-IM-2012-2144/1; Ban-Lao, leg. Messager, MNHN-IM-2012-2146/28; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2147/29; Pakhé, leg. Messager, MNHN-IM-2012-2148/3 ("var. *major*"); Pac-Kha (Pakhé), leg. Messager, MNHN-IM-2012-2155/6 ("var. *major*"); Pac-Kha, leg. Messager, MNHN-IM-2012-2208/3 ("var. *major*"); Ban-Lao, leg. Messager, MNHN-IM-2012-2150/22; Pac-Kha (Pakhé), leg. Messager, MNHN-IM-2012-2157/19; Muong-Kong, leg. Messager, MNHN-IM-2012-2158/10; Pac-Kha (Pakhé), leg. Messager, MNHN-IM-2012-2160/22; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2161/28; Pac-Kha (Pakhé), leg. Messager, MNHN-IM-2012-2168/14; Muong-Kong, leg. Messager, MNHN-IM-2012-2169/10; Muong-Hum, leg. Messager, MNHN-IM-2012-2174/1; Muong-Bo, leg. Messager, MNHN-IM-2012-2178/8; Pac-Kha, leg. Messager, MNHN-IM-2012-2180/4; Tonkin, leg. Messager, MNHN-IM-2012-2182/20; Muong-Hum, leg. Messager, MNHN-IM-2012-2190/7; Long-Ping, leg. Messager, MNHN-IM-2012-2192/11; Long-Ping, leg. Messager, MNHN-IM-2012-2206/16; Pac-Kha, leg. Messager, MNHN-IM-2012-2209/4; Pac-Kha, leg. Messager, MNHN-IM-2012-2210/2; Muong-Kong, leg. Messager, MNHN-IM-2012-2244/1; Pakhé, leg. Messager,

Figure 4. Shells of Vietnamese *Gudeodiscus* species. **A** *Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887), MNHN 24581 (syntype of *Plectopylis phlyaria*) **B** *G.* (*G.*) *phlyarius*, SMF 150125a (lectotype of *Plectopylis moellendorffi*) **C** *G.* (*G.*) cf. *phlyarius*, Vn10-41, coll. PGB **D** *G.* (*G.*) *phlyarius*, Vn09-06, coll. HE **E** *G.* (*G.*) *phlyarius*, NHMUK 1922.8.29.56 (holotype of *Plectopylis gouldingi*) **F** *G.* (*G.*) *phlyarius*, NHMUK 1922.8.29.57 (holotype of *Plectopylis anterides*). Photos: T. Deli (**A**), E. Neubert (**B**), B. Páll-Gergely (**C, D**) and H. Taylor (**F**). Scale represents 10 mm.

Figure 5. Shells of Vietnamese *Gudeodiscus* species. **A** *Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887) (typical "*fallax* var. *major*"), MNHN-IM-2012-2155 **B** *G.* (*G.*) *phlyarius*, NHMUK 1922.8.29.55 (holotype of *Plectopylis verecunda*) **C** *G.* (*G.*) *phlyarius*, NHMUK 1922.8.29.58 (holotype of *Plectopylis fallax*) **D** *G.* (*G.*) *messageri raheemi* Páll-Gergely & Hunyadi, ssp. n., Vn10-76, coll. PGB **E** *G.* (*G.*) *messageri raheemi* ssp. n., NHMUK 20110370.1 (holotype) **F** *G.* (*G.*) *messageri messageri* (Gude, 1909), NHMUK 1922.8.29.53 (holotype) **G** *G.* (*G.*) *messageri messageri* NHMUK 1922.8.29.54 (syntype of *P. messageri* var. *minor*). Photos: B. Páll-Gergely (**A, D**), H. Taylor (**B–C, E–G**). Scale represents 10 mm.

MNHN-IM-2012-2245/9; Cao-Bang, leg. Messager, MNHN-IM-2012-2470/2; Na-Ri, leg. Messager, MNHN-IM-2012-2463/1; Col de Nuages, leg. Messager, MNHN-IM-2012-2451/6; Tonkin, leg. Messager, MNHN-IM-2012-2450/15; Nat-Son, leg. Messager, MNHN-IM-2012-2445/1; Tonkin, leg. Messager, MNHN-IM-2012-2442/2; Bac-Kan, leg. Messager, MNHN-IM-2012-2247/1; Nga-Son, leg. Messager, MNHN-IM-2012-2255/1; Environs de Yen Bai, ex coll. labo. de Géologie de la Sorbonne (entrée 1952), MNHN-IM-2012-2272/1; Pakhé, leg. Messager, MNHN-IM-2012-2340/12; Tonkin, leg. Messager, MNHN-IM-2012-2395/2; Tonkin, leg. Messager, MNHN-IM-2012-2396/2; Muong-Bo, coll. Staadt, 1969, MNHN-IM-2012-2406/4; Tonkin, coll. Letellier, 1949, MNHN-IM-2012-2410/1; Tonkin, coll. Staadt, 1969, MNHN-IM-2012-2412/1; Trinh-Thuong, coll. Staadt, 1969, MNHN-IM-2012-2416/5; Tonkin, coll. Staadt, 1969, MNHN-IM-2012-2420/1; Trinh-Thuong, coll. Lavezzari, 1929, MNHN-IM-2012-2421/10; Tonkin, Pac-Kha, NHMUK 1916.3.16.14/1; Tonkin, Trinh-Thuong, 5/1/09, NHMUK 20130621.1–2/2; Tonkin, Pac-Kha, 14/6/10, NHMUK 20110289/3 (labelled as „*anterides*“); Tonkin, Pac-Kha, coll. Preston, 3/11/08, NHMUK 20110290/2 (labelled as „*moellendorffi*“); Tonkin, Muong-Bo, coll. Salisbury ex Beddome, NHMUK 20110291/3 (labelled as „*fallax=moellendorffi*“); Tonkin, Lao Kay, NHMUK 1920.1.20.15–16/2; Tonkin, Muong-Bo, NHMUK 1909.3.14.18–20/3; Tonkin, Trinh-Thuong, coll. Rosen ex Messager, NHMW 71640/O/9481/1; Tonkin, Haut-Tonkin, Region de Lao-Kay, coll. Rolle, NHMW 92564/2; Tonkin, Muong-Kong, coll. Rušnov ex Rolle ex Messager, NHMW 92565/1; Tonkin, Pac-Kha, NHMW 46226/1; Tonkin, Long-Po (?), coll. Oberwimmer ex Wagner ex Messager, NHMW 92579/1; Tonkin, Muong-Bo, NHMW 46291/2.

***gouldingi*/*anterides*-like shells.** Pakhé, leg. Messager, MNHN-IM-2012-2133/53; Muong-Kong, leg. Messager, MNHN-IM-2012-2141/14; Na-Ri, leg. Messager, MNHN-IM-2012-2152/8; Nat-Son, leg. Messager, MNHN-IM-2012-2153/118; Pac-Kha (Pakhé), leg. Messager, MNHN-IM-2012-2156/4; Pac-Kha (Pakhé), leg. Messager, MNHN-IM-2012-2164/44; Bac-Kan, leg. Messager, MNHN-IM-2012-2167/29; Muong-Kong, leg. Messager, MNHN-IM-2012-2170/1; Tonkin, leg. Messager, MNHN-IM-2012-2175/8; Tonkin, leg. Messager, MNHN-IM-2012-2176/10; Muong-Bo, leg. Messager, MNHN-IM-2012-2179/1; Nac-Ri, leg. Messager, MNHN-IM-2012-2187/6; Muong-Hum, leg. Messager, MNHN-IM-2012-2189/1; Long-Ping, leg. Messager, MNHN-IM-2012-2193/1; Bac-Kan, leg. Messager, MNHN-IM-2012-2195/18; Long-Ping, leg. Messager, MNHN-IM-2012-2197/4; Pac-Kha, leg. Messager, MNHN-IM-2012-2200/32; Pac-Kha, leg. Messager, MNHN-IM-2012-2201/15; Tonkin, leg. Messager, MNHN-IM-2012-2203/1; Long-Ping, leg. Messager, MNHN-IM-2012-2207/4; Long-Ping, leg. Messager, MNHN-IM-2012-2213/2; Cho-Ra, leg. Messager, MNHN-IM-2012-2478/1; Bac-Kan, leg. Messager, MNHN-IM-2012-2476/2; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2473/6; Bac-Kan, leg. Messager, MNHN-IM-2012-2465/4; Na-Ri, leg. Messager, MNHN-IM-2012-2464/1; Na-Ri, leg. Messager, MNHN-IM-2012-2462/8; Tonkin, leg. Messager, MNHN-IM-2012-2459/1;

Pakhé, leg. Messager, MNHN-IM-2012-2454/8; Col de Nuages, leg. Messager, MNHN-IM-2012-2452/15; Nat-Son, leg. Messager, MNHN-IM-2012-2446/1; Col de Nuages, leg. Messager, MNHN-IM-2012-2214/9; Na-Ri, leg. Messager, MNHN-IM-2012-2220/8; Pakhé, leg. Messager, MNHN-IM-2012-2226/5; Tonkin, leg. Messager, MNHN-IM-2012-2228/1; Muang-Kong, leg. Messager, MNHN-IM-2012-2243/7; Nat-Son, leg. Messager, MNHN-IM-2012-2256/12; Phi-Mi, leg. Messager, MNHN-IM-2012-2334/1; Tonkin, leg. Messager, MNHN-IM-2012-2372/3; Muong-Kong, leg. Messager, MNHN-IM-2012-2429/8; Bac-Kan, leg. Messager, MNHN-IM-2012-2433/16; Bac-Kan, leg. Messager, MNHN-IM-2012-2436/1; Tonkin, leg. Messager, MNHN-IM-2012-2422/8; Pakhé, leg. Messager, MNHN-IM-2012-2389/2; Bac-Kan, leg. Messager, MNHN-IM-2012-2404/1; Tonkin, coll. Levazzari, 1929, MNHN-IM-2012-2405/3; Muong-Bo, coll. Staadt, 1969, MNHN-IM-2012-2407/1; Trinh-Thuong, coll. Levazzari, 1929, MNHN-IM-2012-2409/1; Bac-Kan, leg. Messager, MNHN-IM-2012-2438/1; Tonkin, leg. Messager, MNHN-IM-2012-2439/6; Tonkin, Pac-Kha, coll. Kennard, A.S. ex auct. (Gude), NHMUK 20130620/1; Tonkin, Pac-Kha, coll. Salisbury ex Beddome, NHMUK 20110285/1 ("*gouldingi* var. *minor*"); Tonkin, Pac-Kha, coll. Preston, 3/11/08, NHMUK 20110286/2; Tonkin, Pac-Kha, coll. Salisbury ex Beddome, NHMUK 20110287/2 ("*anterides*"); Tonkin, Pac-Kha, coll. Preston, 3/11/08, NHMUK 20110288/2 ("*anterides*"); Tonkin, Pac-Kha, 1909.3.17.21-23/3 ("*anterides*"); Tonkin, Long-Ping NHMUK 1916.3.16.3/1 ("*anterides*"); Tonkin, Pac-Kha, Tonkin, Pac-Kha, NHMUK 1909.3.17.26-28/3; Tonkin, Pac-Kha, coll. Rosen ex Messager, NHMW 71640/O/9478/2; Tonkin, Bac-Kha, coll. Rušnov ex Rolle ex Messager, NHMW 92566/2; Tonkin, Pac-Kha, NHMW 46225/2; Tonkin, Pac-Kha, coll. Wagner ex Messager, NHMW 71640/O/10290/1; Tonkin, Long-Phai, coll. Wagner ex Messager, NHMW 71640/O/10291/1; Tonkin, Pac-Kha, NHMW 92568/1; Tonkin, Pac-Kha, NHMW 46292/2; Tonkin, Bac-Kan, coll. Wagner ex Messager, NHMW 71640/O/10292/1; Tonkin, Bac-Kan, coll. Oberwimmer, NHMW 71640/O/14029/3; Tonkin, Nat-Son, coll. Rušnov ex Messager, NHMW 103354/1.

"Mixed" *gouldingi*/*anterides*/*fallax* samples. Bac-Kan, leg. Messager, MNHN-IM-2012-2171/20; Trinh-Thuong, leg. Messager, MNHN-IM-2012-2181/44; Pakhé, leg. Messager, MNHN-IM-2012-2185/31; Muong-Bo, leg. Messager, MNHN-IM-2012-2211/3; Col de Nuages, leg. Messager, MNHN-IM-2012-2218/25; Col de Nuages, leg. Messager, MNHN-IM-2012-2222/15; Tonkin, leg. Messager, MNHN-IM-2012-2224/13; Tonkin, Pac-Kha, coll. Dosch ex Rolle ex Messager, SMF 172079/4.

***phlyarius*-like shells.** Tonkin, Than-Moi, coll. Jetschin, SMF 207669/6; Tonkin, Than-Moi, coll. Möllendorff ex Fruhstorfer, SMF 150126/10; Tonkin, Chuot-Ki (?), coll. Jaeckel, S. H., SMF 207676/1; Tonkin, coll. Ehrmann ex Fruhstorfer, SMF 150127/2; Tonkin, Than-Moi, coll. Dosch ex Rolle, SMF 172092/4; Tonkin, Than-Moi, coll. Dosch ex Rolle, SMF 172091/4; Tonkin, Than-Moi, coll. Dosch ex Rolle, SMF 172093/2; Tonkin, Than-Moi, coll. Ehrmann ex Fruhstorfer, H., SMF 150138/1+1jb; Than-Moi, leg. Messager, MNHN-IM-2012-2212/5; Long-Phai, leg. Messager, 1901, MNHN-IM-2012-2232/1; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2279/4; Tonkin, coll. Weiss, 1901, MNHN-IM-2012-2281/5; Province de Cao Lang, Lang-Son, Ky Lua, coll. Saurin, MNHN-IM-2012-2288/2; Na-Ri, leg. Messager, MNHN-IM-2012-2474/1; Tonkin, leg. Messager, MNHN-IM-2012-2427/3; Tonkin, leg. Messager, MNHN-IM-2012-2431/1; Tonkin, leg. Messager, MNHN-IM-2012-2391/1; Bac-Kan, coll. Staadt, 1969, MNHN-IM-2012-2392/2; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2397/5; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2398/1; Lang-Son, coll. Letellier, 1949, MNHN-IM-2012-2401/1; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2413/8; Tonkin, coll. Denis, 1946, MNHN-IM-2012-2387/4; Tonkin, Pac-Kha, NHMUK 1916.3.16.13/1; Tonkin, coll. Salisbury ex Beddome, NHMUK 20130599/2; Tonkin, Muong-Bo, 3/11/08, NHMUK 20130600/2; Tonkin, 4/11/01/32, NHMUK 20130601/3; Tonkin, Phu Quac Oai, coll. Biggs, H.E.J., Acc. no. 2258, NHMUK 20130602/4; Tonkin, coll. Trechmann, Acc. no. 2176, NHMUK 20130603/2; Tonkin, Than-Moi, leg. Fruhstorfer, H., NHMUK 1901.12.12.206–208/3; Tonkin, „showing immature armature“, coll. Gude, G.K, NHMUK 1916.3.15.3/1; Tonkin, coll. Fruhstorfer, NHMW 40850/2; Tonkin, coll. Rušnov ex Blume, NHMW 92562/2; Tonkin, Than-Moi, NHMW 39292/4; Tonkin, Than-Moi, coll. Klemm, NHMW 79000/K/17483/1; Tonkin, Than-Moi, coll. Rušnov ex Rolle ex Messager, NHMW 92580/2; Tonkin, Than-Moi, coll. Rušnov ex Rolle, NHMW 92581/4; Tonkin, Than-Moi, coll. Rolle, NHMW 71640/O/12301/1; Tonkin, Than-Moi, coll. Edlauer, NHMW 75000/E/38490/3; Tonkin, That-Ké, coll. Oberwimmer, NHMW 71640/O/12300/1; Tonkin, coll. Fruhstorfer, NHMW 40851/1; Tonkin, That-Ke, coll. Oberwimmer, NHMW 92560/2; Tonkin, Bac-Khuon, coll. Rolle, NHMW 50857/1 (mixed sample with *giardi*).

***verecunda*-like shells.** Phong-Tho, leg. Messager, MNHN-IM-2012-2177/9; Nat-Son, leg. Messager, MNHN-IM-2012-2447/6; Phong-Tho, leg. Messager, MNHN-IM-2012-2443/4; Phong-Tho, leg. Messager, MNHN-IM-2012-2423/4; Lai-Chau, coll. Morlet, MNHN-IM-2012-2424/1; Son-Ma, coll. Fischer, MNHN-IM-2012-2417/1.

New material examined. *fallax*-like shells. 2011/125 Lào Cai Province, 1.5 km N of Bắc Ngầm cross, valley on the left side of the road, 155 m, 22°24.149'N, 104°14.462'E, leg. Hunyadi, A., 02.12.2011., HA/1; **Vn11-187** Lào Cai Province, ca. 3 km SW of Nhà Văn Hóa, 22°25.513'N, 104°12.194'E, leg. Hemmen, Ch. & J., 04.10.2011., HE/21 (+2 specimens in ethanol, one of them anatomically examined, Figures 21, 28A).

***phlyarius*-like shells. Vn10-53** Lạng Sơn Province, right off rd. 1B Long Đống to Bình Gia, 21°53.938'N, 106°25.605'E, leg. Hemmen, Ch. & J., 20.3.2010., PGB/3; **Vn10-48** Lạng Sơn Province, ca. 6 km SE Bắc Sơn (rd. Bắc Sơn to Nga Hải, left off rd), 21°52.422'N, 106°21.508'E, leg. Hemmen, Ch. & J., 19.03.2010., PGB/3; **Vn09-24** Cao Bằng Province, ca. 1 km N of Mã Phục (right side off rd. 3), ca. 575 m, 22°43.938'N, 106°20.527'E, leg. Hemmen, Ch. & J., 23.03.2009., HE/1, PGB/3;

Vn10-49 Lạng Sơn Province, ca. 16 km SE Bắc Sơn (rd. Bắc Sơn to Nga Hải, left off rd), 21°50.019'N, 106°18.405'E, leg. Hemmen, Ch. & J., 19.03.2010., PGB/2+2jb; **Vn09-18** Lạng Sơn Province, ca. 27 km S of Thất Khê, right side off rd. #4 (Lạng Sơn-Thất Khê), ca. 300 m, 22°07.484'N, 106°35.427'E, leg. Hemmen, Ch. & J., 13.10.2009., PGB/7; **Vn09-19** Lạng Sơn Province, ca. 25 km S of Thất Khê, right side off rd. #4 (Lạng Sơn-Thất Khê), ca. 220 m, 22°06.477'N, 106°35.356'E, leg. Hemmen, Ch. & J., 13.10.2009., PGB/2; **Vn10-129** Lạng Sơn Province, ca. 58.5 km from Thái Nguyên to Bắc Sơn (right side off road), 21°51.166'N, 106°13.003'E, leg. Hemmen, Ch. & J., 22.10.2010., PGB/1; **Vn10-56** Lạng Sơn Province, ca. 7 km from Đồng Mỏ to Văn Quan (left off rd #279), no GPS data, approximate GPS position: 21.696000°N, 106.547271°E, leg. Hemmen, Ch. & J., 21.3.2010., PGB/5; **Vn09-16** Lạng Sơn Province, Tân Mỹ (N of Lạng Sơn), temple south of the entrance of village, ca. 240 m, 21°58.891'N, 106°40.265'E, leg. Hemmen, Ch. & J., 12.10.2009., PGB/3; **Vn10-128** Lạng Sơn Province, ca. 69 km from Thái Nguyên to Bắc Sơn (right side off road), 21°54.270'N, 106°15.801'E, leg. Hemmen, Ch. & J., 22.10.2010., HE/8, PGB/9; **Vn11-154** Lạng Sơn Province, km 47, 1 road # 1B between Văn Quan and Bắc Sơn, 21°52.785'N, 106°26.262'E, leg. Hemmen, Ch. & J., 01.04.2011., HE/6 (also in ethanol); **Vn11-155** Lạng Sơn Province, ca. 55 km from Bình Gia to Lạng Sơn on road 1B (no GPS data), leg. Hemmen, Ch. & J., 01.04.2011., HE/11; **Vn11-156** Lạng Sơn Province, ca. 10.6 km from Bình Gia to Lạng Sơn on road 1B, 21°53.639'N, 106°25.895'E, leg. Hemmen, Ch. & J., 01.04.2011., HE/70 (one of them is sinistral!), (anatomically examined, Figures 22, 28C, 35J–L); **Vn11-157** Lạng Sơn Province, ca. km. 50 of road 1B, 10 km to Bình Gia, 21°53.911'N, 106°25.664'E, leg. Hemmen, Ch. & J., 01.04.2011., HE/6 (anatomically examined, see Figure 31C); **2011/65** Lạng Sơn Province, Đồng Mỏ 2.5 km towards Văn Quan, right side of the road, 270 m, 21°40.358'N, 106°34.783'E, leg. Hunyadi, A., 10.11.2011., HA/5; **2011/66** Lạng Sơn Province, Đồng Mỏ 4.5 km towards Văn Quan, left side of the road, 330 m, 21°40.828'N, 106°34.531'E, leg. Hunyadi, A., 10.11.2011., HA/23, PGB/2; **2011/67** Lạng Sơn Province, Đồng Mỏ 6 km towards Văn Quan, left side of the road, 390 m, 21°41.034'N, 106°33.618'E, leg. Hunyadi, A., 10.11.2011., HA/20, PGB/2; **2011/68** Lạng Sơn Province, Đồng Mỏ 7 km towards Văn Quan, Vạn Linh cross., left side of the road, 370 m, 21°41.158'N, 106°33.588'E, leg. Hunyadi, A., 10.11.2011., HA/56, PGB/3; **2011/70** Lạng Sơn Province, Lạng Sơn, NNE side of Núi Vọng Phu, 21°51.183'N, 106°44.950'E, leg. Hunyadi, A., 11.11.2011., HA/3; **2011/72** Lạng Sơn Province, Na Sầm 12 km towards Thất Khê, left side of the road 210 m, 22°07.870'N, 106°35.038'E, leg. Hunyadi, A., 12.11.2011., HA/86, PGB/2; **2011/73** Lạng Sơn Province, Na Sầm 10 km towards Thất Khê, left side of the road, 190 m, 22°07.530'N, 106°35.381'E, leg. Hunyadi, A., 12.11.2011., HA/27, PGB/2; **2011/74** Lạng Sơn Province, Na Sầm 5.5 km towards Thất Khê, right side of the road, 165 m, 22°05.466'N, 106°35.425'E, leg. Hunyadi, A., 12.11.2011., HA/10; **2011/75** Lạng Sơn Province, Tân Mỹ, tunnel 200 m towards Na Sầm, 210 m, 21°59.110'N, 106°40.077'E, leg. Hunyadi, A., 12.11.2011., HA/19, PGB/2; **2011/76** Lạng Sơn Province, northern edge of Chi Lăng, pass next to the tourist path (N of Đồng Bành), 75 m, 21°34.945'N, 106°30.567'E, leg. Hunyadi, A., 13.11.2011., HA/1; **2011/78** Lạng Sơn Province, Đồng Mỏ 7 km towards Chi Lăng, right side of the road, leg. Hunyadi, A., 13.11.2011., HA/1; **2011/79** Lạng Sơn Province, Đồng Mỏ 5.2 km towards Chi Lăng, right side of the road, 40 m, 21°37.215'N, 106°32.538'E, leg. Hunyadi, A., 13.11.2011., HA/1; **2012/37** Lạng Sơn Province, Đồng Mỏ 2.7 km towards Chi Lăng, right side of the old road, cave, 70 m, 21°38.286'N, 106°33.391'E, leg. Hunyadi, A., 25.05.2012., HA/10; **2012/38** Lạng Sơn Province, Đồng Mỏ 4–5 km towards Chi Lăng, right side of the old road, 65 m, 21°37.479'N, 106°32.730'E, leg. Hunyadi, A., 25.05.2012., HA/6; **Vn11-159** Lạng Sơn Province, at km 74.8 on road 1B, Đồng Đăng to Thái Nguyên (8 km S Bắc Sơn), 21°54.543'N, 106°17.298'E, leg. Hemmen, Ch. & J., 02.04.2011., HE/1; **Vn11-158** Lạng Sơn Province, ca. 7.5 km foad 1B from Bình Gia to Bắc Sơn, 21°53.908'N, 106°25.661'E, leg. Hemmen, Ch. & J., 01.04.2011., HE/1; **Vn09-06** Ninh Bình Province, Cúc Phương Nat. Park, ca. half way from Park Headquarters to Thousand Year Old Tree, left path, ca 510 m, 20°21.366'N, 105°35.513'E, leg. Hemmen, Ch. & J., 03.10.2009., HE/2; **MAA10** Ninh Bình Province, Cúc Phương Nat. Park, path to fairy cave, 20°21'N, 105°54'E (approximate GPS position), leg. Vermeulen, J., coll. Maassen, W.J.M., 10.10.1998., NHMUK 19991444/2 + one juvenile/broken shell (marked with no. 3 on Figure 43); same data, WM/3; **Vn10-41** Thái Nguyên Province, Temple Chùa Hang (ca. 1 km S of Chợ Chu), 21°54.070'N, 105°38.856'E, leg. Hemmen, Ch. & J., 16.03.2010., HE/3 (marked with no.2 on Figure 43).

Diagnosis. The species is very variable in terms of shell characters (spire height, presence/absence of the apertural fold, aperture shape, morphology of the parietal and palatal plicae and lamellae, fine morphology of the periostracum folds) between and within traditionally recognized species which are synonymized here. Therefore, it is impossible to give a general diagnosis.

Measurements (in mm). D = 19.3–20.2, H = 8.8–9.1 (n=3, "*fallax*", MNHN 2012-2155); D = 10.6–11.7, H = 4.5–4.7 (n=4, "*gouldingi*", MNHN, IM-2012-2164); D = 13.2–13.4, H = 5.9–6 (n=2, "*phlyarius*", Vn10-53); D = 14.7–15.5, H = 7.8–8.5 (n=3, "*phlyarius*", Vn09-18); D = 12.4–12.7, H = 5.7–5.8 (n=2, "*phlyarius*", MAA10); D = 15.5–17.1, H = 7.7–7.8 (n=2, "*phlyarius*", Vn10-56); D = 15.8–16.6, H = 8.8–9 (n=3, *verecunda*, MNHN 2012-2177). The size range is continuous to from typical *anterides*/*gouldingi* to *fallax* var. *major* (see Figure 16).

Differential diagnosis. See under *Gudeodiscus anceyi*, *G. emigrans*, *G. giardi*, *G. hemmeni* sp. n., *G. messageri* and *Halongella fruhstorferi*.

Intrasubspecific diversity. Extremely large. Table 9 summarized the conchological differences between newly collected Vietnamese *Gudeodiscus phlyarius* samples.

Description of the genitalia. Typical *fallax*: Two specimens were anatomically examined. Locality: Lào Cai Province, ca. 3 km SW of Nhà Văn Hóa, 22°25.513'N, 104°12.194'E, leg. Hemmen, Ch. & J., 04.10.2011. (Figures 21, 28A);

Penis rather spindle-shaped, very much thickened in the middle; internally with a fine papillated/reticulated structure (proximal part) which gradually becomes a laterally folded structure with flat calcareous granules between the folds; pockets are ar-

Table 9. Diversity of shell characters within newly collected Vietnamese *Gudeodiscus* (*Gudeodiscus*) *phlyarius*. Abbreviations: OCMA: only corroded material available.

code	spire	aperture shape	periostracal folds
Vn11-187	flat	elongated	normal
2011/66	slightly elevated	rounded	pointed
2011/67	flat/slightly elevated	rounded	pointed
2011/68	slightly elevated	rounded	pointed
2011/70	slightly elevated	rounded	OCMA
2011/72	slightly elevated	rounded	normal
2011/73	slightly elevated	rounded	OCMA
2011/75	flat/slightly elevated	rounded	normal
Vn09-16	slightly elevated	rounded	OCMA
Vn09-18	slightly elevated	rounded	normal
Vn09-19	slightly elevated/ elevated	rounded	OCMA
Vn09-24	flat/slightly elevated	rounded	OCMA
Vn10-128	flat/slightly elevated	rounded	normal
Vn10-129	slightly elevated	rounded	normal
Vn10-48	flat/slightly elevated	rounded	OCMA
Vn10-49	flat/slightly elevated	rounded	pointed
Vn10-53	flat	rounded	pointed
Vn10-56	flat/slightly elevated	rounded	pointed

ranged in a rather straight line; epiphallus much shorter than penis, thickest at the penis-epiphallus transition, slowly becoming slimmer towards the vas deferens; penis and epiphallus connected with weak muscle fibres; penial caecum absent in one of the specimens and very small in the other; retractor muscle thick, short, inserts on the small penial caecum (or on the penis-epiphallus transition of the other specimen); vas deferens very long; the proximal section curves within a translucent, straight tube, most convolutions occurring proximally to the vaginal bulb, before becoming a solid, thick tube (until the sperm-oviduct). Vagina long, centrally with well-developed vaginal bulb; vaginal bulb thick-walled, internally with fine reticulated sculpture; distal part of the vagina internally with low, dense, transversal folds; gametolytic sac and diverticulum long, of equal length, extending in parallel; gametolytic sac spindle-shaped, diverticulum of equal thickness throughout.

typical *phlyarius*: Two specimens were anatomically examined, both contained a few embryos at an early developmental state. Localities: Lạng Sơn Province, ca. 10.6 km from Bình Gia to Lạng Sơn on road 1B, 21°53.639'N, 106°25.895'E, leg. Hemmen, Ch. & J., 01.04.2011. (Figures 22, 28C); Lạng Sơn Province, ca. km. 50 of road 1B, 10 km to Bình Gia, 21°53.911'N, 106°25.664'E, leg. Hemmen, Ch. & J., 01.04.2011. (Figure 31C).

Penis spindle-shaped with thickened middle section; internally with elongated folds of various thickness; this internal ribbed surface also continues in the small penial caecum; retractor muscle short, inserts on the penial caecum; epiphallus shorter and much slimmer than the penis; distally the penis and proximal part of epiphallus bound with connective tissue; vas deferens very long, proximally simple, slim, curved centrally and covered with a sheath distally simple and thickened. Vagina long with well-developed central vaginal bulb; internally the proximal part of the bulb is almost smooth; this sculpture changes to parallelly folded structure in distal direction (Figure 31C); the distal part of the vagina is strongly folded; gametolytic sac and diverticulum of equal length, both being relatively short.

Radula. See Table 6 and Figures 35J–L.

Distribution (see Figure 43). The populations assigned to *Gudeodiscus phlyarius* inhabit several regions of northern Vietnam (Lạng Sơn, Cao Bằng, Ninh Bình, and along the border region with the Chinese Yunnan Province) and the Chinese Guangxi. A single shell of typical *P. fallax* Gude, 1909 was collected in southern Yunnan, very close to the Vietnamese border (Honghe Hanizu Yizu Zizhizhou, Hekou Yaozu Zizhixian, Laofanzhai Xiang, Sierqi N 1.5 km towards Laofanzhai, 155 m, 22°44.637'N, 103°53.782'E, leg. Hunyadi, A., 19.03.2011., HA/1).

Remarks. *Gudeodiscus phlyarius* and taxa of similar appearance are one of the most problematical groups in the Plectopylidae. Gude (1909) described six species (*anterides*, *cyrtochila*, *fallax*, *gouldingi*, *messageri*, *verecunda*) from the border region of northern Vietnam with the Chinese Yunnan Province. One species, *Plectopylis cyrtochila* differs from the rest of the species by the smooth, lenticular shell and week peristome and callus. Therefore, it is discussed separately, under the name *G. cyrtochilus*. In face of the obvious similarities between the remaining five species, *Plectopylis messageri* and *P. fallax* were only compared with *P. moellendorffi*, and *P. verecunda* was compared with *P. messageri*. The shell characters of *P. anterides* and *P. gouldingi* were only compared with each other. Shells having transitional characters were explained by hybrid origin. Gude (1909) mentions that a specimen of *messageri* from Pac-Kha might be a hybrid with *moellendorffi*, and another specimen from the same locality was believed to be a hybrid of *anterides* and *gouldingi*. The shell characters distinguishing *G. messageri* and the sympatric species referable to *fallax*, *gouldingi* and *anterides* are stable, therefore *G. messageri* is handled separately from the rest of the taxa.

In the recent revision of the Chinese members of the family (Páll-Gergely and Hunyadi 2013), *Gudeodiscus phlyarius* was reported from several localities in Guangxi. *Plectopylis moellendorffi* Gude, 1901 was synonymized with *P. phlyarius*. *Gudeodiscus phlyarius werneri* was described from two nearby localities near Duan city. All other Chinese *G. phlyarius* populations were assigned to the nominotypical subspecies. *Gudeodiscus phlyarius phlyarius* populations were listed in two separate groups based on their appearance, namely "*phlyarius*-like, mainly flat, small form" and "larger, strongly-built shell (transition to *werneri*)".

Here we include the following taxa as synonyms of *Gudeodiscus phlyarius*: *anterides* Gude, 1909, *fallax* Gude, 1909, *fallax* var. *major* Gude, 1909, *gouldingi* Gude, 1909, *moellendorffi* Gude, 1901, *verecundus* Gude, 1909, *werneri* Páll-Gergely, 2013. The last taxon was described on the basis of a keel with a light band around the umbilicus, the dissolved anterior lamella, the posteriorly elongated upper and lower ends of the posterior lamella and the parallel, horizontal palatal plicae. All other formerly recognized species (*anterides*, *fallax*, *gouldingi*, *moellendorffi*, *verecundus*) have two well-developed lamellae and oblique, usually depressed Z-shaped palatal plica, often with Y-like posterior ends. However, this study revealed that *G. phlyarius* is a widely distributed, very variable species and at this moment we see no good reason to maintain one of the morphologically distinct forms as a subspecies. Consequently, we synonymize *G. phlyarius werneri* with *G. phlyarius*.

According to the original description the anterior lamella of *gouldingi* is simple whereas that of *anterides* is "provided with buttresses". The upper parietal plica is in contact with the anterior lamella in *gouldingi*, but the lamella is shorter and free in *anterides*. Both the upper and lower plicae are shorter in *anterides*. The first palatal plica of *anterides* has a descending ridge; the same plica is straight in *gouldingi*. Additionally, the palatal plicae of *anterides* are not united by a vertical ridge and are more widely spaced than in *gouldingi* (the drawings in the original description show the reverse). All of the differences mentioned by Gude (1909) are unstable even within a single sample (assumed to be single population). For example, six shells were opened from a sample collected in Nat-Son (leg. Messager, MNHN-IM-2012-2153, containing 118 "*gouldingi*" shells). The length of the lower horizontal plica varies greatly, but extends beyond the anterior lamella in the anterior direction in every cases. One specimen had buttresses on the anterior lamella. Two specimens possessed an anterior lamella and the upper horizontal plica united, whereas in the case of four specimens this plica was free. Even among the few shells examined by Gude, he found that shells exhibited transitional character states between *anterides* and *gouldingi*. Therefore, these forms cannot be handled as separate species.

In the original description of *Plectopylis fallax*, Gude (1909) compared it only with *P. moellendorffi*. He did not compare *P. fallax* either with *P. anterides*, or with *P. gouldingi*. Based on the material housed in the NHM and the specimens mentioned in Gude's (1909) paper, Gude received very few shells from Messager. Examining the type specimens of the above-mentioned taxa revealed that besides the difference in size (typical *fallax* is larger than *anterides* and *gouldingi*), the only distinguishing feature is the simple and free palatal plicae in *fallax* and the bifurcated and usually connecting plicae of *gouldingi* (syn: *anterides*). The palatal plicae are very variable even within the same sample (see Figures 11) and certainly cannot be used to separate these taxa. Larger shells usually have separated palatal plicae and smaller shells tend to have joint palatal plicae. In addition, the characteristic "nautiliform" shape of typical *fallax* shells is also not a reliable distinguishing feature from *Plectopylis gouldingi*/*anterides* as this trait is also variable across *gouldingi* and *fallax* samples.

Based on shell size, most of Messager's samples in the MNHN can be assigned to three forms (approximately 11–13 mm: *gouldingi*, 14–16 mm: *fallax*, 19–21 mm: *fallax* var. *major*). However, the ranges of shell size overlaps within a few samples (see "mixed" samples under the material) and assigning some of these shells to one of the forms is impossible. The size range from typical *gouldingi* (11 mm) to *fallax* var. *major* (21 mm) shows a clinal variation without interruption (see Figure 16). On the other hand, we found one sample where the shells clearly differ from two separate forms, namely six typical "*fallax* var. *major*" (D: 18.9–20 mm) and *gouldingi* (D: 12.4–13.5) shells. Unfortunately, as in other samples, the collection locality is not exact enough to determine if these specimens were sympatric.

The apertural fold is always present on typical *Gudeodiscus phlyarius* shells, but can be rudimentary or missing in typical *anterides*/*fallax*/*gouldingi* shells. The edge of the periostracal folds has a pointed structure which seems to occur in a spiralling pattern on the shell of most Vietnamese *phlyarius* specimens, but these are always missing in *fallax* and *gouldingi* specimens (this trait is visible only in fresh shells) (Figures 10C–F). Typical *moellendorffi* specimens (synonym of *phlyarius*) possess a somewhat elevated spire, whereas typical *anterides*/*fallax*/*gouldingi* shells are almost always entirely flat. The only shell character found to be stable within typical Vietnamese *Plectopylis phlyarius* shells and *Plectopylis anterides*/*fallax*/*gouldingi* shells, however, is the rounded aperture in the former and the elongated aperture in the latter (Figures 9C–D). Even this difference is found to be variable in Chinese populations. The populations listed as "transitions to *werneri*" in Páll-Gergely and Hunyadi (2013) have rather elongated aperture, similar to that of typical Vietnamese *fallax* shells, but have elevated spire and overall similar shell shape to typical Vietnamese *phlyarius*. Therefore, we refer to *anterides*, *gouldingi* and *fallax* as synonyms of *G. phlyarius*.

The genital structure of typical *fallax* and typical *phlyarius* differ considerably. Namely, the former lacks the penial caecum or has only a very small one, and has a reticulated inner surface of the penis, whereas the latter has a short penial caecum and its penis has parallel folds on the inner wall. The size of the penial caecum however, may not have a strong taxonomic value because it was found to vary largely within species (e.g. *Gudeodiscus multispira*, see Páll-Gergely and Asami 2014). The sculpture of the wall of the proximal portion of the penis may have a seasonal variability (see under *G. villedaryi* and in Discussion).

A sample (MNHN 2012-2177) labelled *verecunda*, which contained 9 shells from the type locality (Phony-Tho) supports the synonymy of the taxon in relation to *gouldingi* and *fallax*, and therefore to *Gudeodiscus phlyarius*. Seven of the shells were typical *verecundus* with an elevated spire, a strong apertural fold connected to the callus, and an anterior lamella fused to the lower plica; the plica does not extending beyond the lamella anteriorly (confirmed in 3 shells). The two other shells however, have somewhat lower spires, the apertural fold is not connected to the callus and the lower plica is free from the anterior lamella and extended beyond it anteriorly (one of the two shells was opened). These two shells can be interpreted as transitional forms between *verecundus* and *fallax* in terms of spire height, apertural fold and parietal plicae/lamellae morphology. Since transitional forms were found between typical *verecunda* and *fallax* shells, *P. verecunda* can be interpreted as a local form of *fallax* having elevated spire and fused anterior lamella and lower plica. Therefore, we synonymise *Plectopylis verecunda* with *G. phlyarius*.

There are two Vietnamese "forms" of *Gudeodiscus phlyarius* which differ from all other typical Vietnamese *phlyarius* shells. One of the morphologically distinct forms inhabits Ninh Bình Province, where we have knowledge of two populations (number 3 on Figure 43). These shells are smaller and comparatively flatter than the usual *phlyarius*, and have a characteristic "nautiliform" shape, wider umbilicus, with the last whorl leaving the larger part of the penultimate whorl visible. No differences in the lamellae were recognized. The other form is known from one locality in north-western Thái Nguyên Province (number 2 on Figure 43). This has an elevated spire and narrow umbilicus. Only three specimens are known, and two of them were opened. One of the opened specimens had three very weak parietal lamellae (possibly an abnormal character state, similar to that of the holotype of *Plectopylis infralevis*), and the second has the anterior lamella and the lower plica fused; the plica did not extends beyond the anterior lamella in the anterior direction.

Two Chinese populations (near Baxianyan, number 1 on Figure 43) have an oblique anterior lamella and an aperture more reflected downwards.

Gudeodiscus (*Gudeodiscus*?) *suprafilaris* (Gude, 1908)

Figures 9A–B, 9R, 14S–Y

1908 *Plectopylis suprafilaris*, — Gude, Journal de Conchyliologie, 55: 353–355., Figs 4a–e, Plate 7, Figs 7–9. [“Quang Huyen”].

2013 *Gudeodiscus suprafilaris*, — Páll-Gergely & Hunyadi, Archiv für Mollusken-kunde, 142 (1): 8.

Types examined. Tonkin, Quang-Huyen, leg. Mansuy, MNHN 24586 (holotype?, Figure 9A).

Museum material examined. Nga-Son, leg. Messager, MNHN-IM-2012-2234/2; Nga-Son, leg. Messager, MNHN-IM-2012-2254/3.

New material examined. Vn10-125 Cao Bằng Province, ca 60 km from Cao Bằng to Bảo Lạc (right side off road), 22°39.494'N, 105°51.059'E, leg. Hemmen, Ch. & J., 19.10.2010., PGB/1; **2011/70** Lạng Sơn Province, Lạng Sơn, NNE edge of Vọng Phu Mountain, 21°51.183'N, 106°44.950'E, leg. Hunyadi, A., 11.11.2011., HA/1jb; **2011/81** Cao Bằng Province, Đèo Mã Phục (pass) 500 m towards Quảng Uyên, left side of the road, rock cavern, 610 m, 22°43.981'N, 106°20.333'E, leg. Hunyadi, A., 14.11.2011., HA/73+10jb, PGB/3 (see Figure 9B); **2011/85** Cao Bằng Province, Cao Bằng 34.5 km towards Đông Khê, left side of the road, 500 m, 22°27.487'N, 106°25.047'E, leg. Hunyadi, A., 15.11.2011., HA/4jb; **2012/44** Cao Bằng Province, southern edge of Pắc Rảo, Trùng Khánh 3 km towards Quảng Uyên, left side of the road, 570 m, 22°48.961'N, 106°30.533'E, leg. Hunyadi, A., 28.05.2012., HA/1; **Vn10-67** Cao Bằng Province, right off old rd. 4A, ca 29 km from Cao Bằng to Đông Khê, 22°28.737'N, 106°21.767'E, leg. Hemmen, Ch. & J., 26.03.2010., HE/2.

Diagnosis. Shell small, discoid-globular, with weak apertural lip and usually a small denticle in the aperture (Figure 9R). The sudden change of the shell sculpture (reticulated above, smooth below) is very characteristic of this species. For the morphology of the plicae see Remarks and Figures 14S–Y.

Measurements (in mm). D = 13.1, D = 7.3 (n=1, Vn10-125); D = 11.1–12.1, H = 6.2–6.3 (n=3, 2011/81); D = 12–14.1, H = 6.2–7.2 (n=2, Vn10-67).

Table 10. Diversity of shell characters within *Gudeodiscus* (*Gudeodiscus*?) *suprafilaris*. Abbreviations: OCMA: only corroded material available.

code	spire	anterior lamella	posterior lamella	palatal plicae	changing line of the sculpture
type series	high	short	present	long, united	middle line of the body whorl
2011/81	moderately high	long	present	long, united	lower than the middle line of the body whorl
2012/44	moderately high	unknown	unknown	short, free	middle line of the body whorl
Vn10-125	high	long	absent	only vertical line visible	middle line of the body whorl
Vn10-67	moderately high	unknown	unknown	short, united	lower than the middle line of the body whorl
2011/85	high	short	present	short, free	lower than the middle line of the body whorl
2011/70	high	short	present	short, free	OCMA

Differential diagnosis. The shell shape of *Gudeodiscus suprafilaris* is similar to that of *G. infralevis*, but *G. suprafilaris* has more regular whorls, a more elevated spire and its sculpture changes suddenly from reticulated dorsally to smooth basally on the last whorl. The sudden change of the sculpture and the almost globular shell distinguishes the species from other species (*G. eroessi*, *G. multispira*, *G. soosi*, *G. yunnanensis*, *G. cyrtochilus* and *G. fischeri*). The Chinese *G. eroessi hemisculptus* Páll-Gergely & Hunyadi, 2013 and *G. yanghaoi* which have similar sculpture are larger, have a flatter shell and different lamellation.

Intraspecific diversity. The species is very variable in terms of spire height, the formation of parietal and palatal plicae and lamellae, and the extent of the sculptured portion on the dorsal side of the shell. The distinctive aperture shape, minute apertural fold and the unique sculpture render this species distinctive and easy to identify. See also Remarks and Table 10.

Distribution (see Figure 41). Examined material was from only Cao Bằng and Lạng Sơn Provinces. The type locality (Quang-Huyen) lies in Cao Bằng Province (see Figure 39).

Remarks. The palatal and parietal plicae and lamellae exhibit extreme variability between populations. The holotype exhibits relatively long, horizontal palatal plicae connected with a ridge; the parietal side possesses a well-developed posterior lamella, upper and lower plica, and a reduced, short anterior lamella (Figures 14S–T). The museum specimens we examined (probably from the same sample as the holotype) had similar palatal plicae and also a reduced anterior lamella. Two examples collected close to the type locality (2011/81, see Figures 14U–V and 2012/44) were examined. Shells belonging to both populations had identical palatal plicae to those of the holotype, but in contrast, had a much longer anterior lamella, free from the lower plica or almost united to it. Additionally, in the type series, the sculptured dorsal surface changes to a smooth surface at around the middle line of the body whorl. In contrast, in the two newly-collected samples the change between the two different sculptures occurs lower, closer to the umbilicus.

In a shell from another population (Vn10-125, see Figures 14X–Y) the palatal plicae were greatly reduced in length so that when viewed through the semi-transparent shell, they appear as though only a single vertical plica was present. The parietal wall of the same shell was ornamented by a strong anterior lamella entirely fused with the lower plica; the posterior lamella was absent, its position was indicated only by a very slight elevation within the structure of the shell.

***Gudeodiscus* (*Gudeodiscus*) *villedaryi* (Ancey, 1888)**

Figures 8B–D, 9J, 10B, 13V–Y, 23–24, 28F–G, 30A–C, 30F, 32D, 35M–O

1888 *Plectopylis Villedaryi* Ancey, Le Naturaliste 2 (10): 71–72., Fig. 2. ["Région de Lang-son et de Bac-ninh"].

1897b *Plectopylis villedaryi*, — Gude, Science Gossip, 4: 139., Figs 60 a–b. ["Lang-son and Bac-ninh, Tonkin"].

1899a *Plectopylis villedaryi*, — Gude, Science Gossip, 5: 332.

1899c *Plectopylis* (*Endoplon*) *villedaryi*, — Gude, Science Gossip, 4: 148.

1899d *Plectopylis* (*Endoplon*) *villedaryi*, — Gude, Science Gossip, 6: 175.

1900 *Plectopylis Villedaryi*, — Gude, The Annals and Magazine of Natural History, 7 (5): 313.

1901c *Plectopylis villedaryi*, — Gude, Journal of Malacology, 8: 116–117., Figs 5a–e. ["Than-Moi"].

1901 *Plectopylis* (*Endoplon*) *choanomphala* Möllendorff, Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft, 33 (5/6): 75. ["Than-moi"].

1901c *Plectopylis* (*Endoplon*) *villedaryi*, — Gude, Journal of Malacology, 8: 116–117., Figs 5a–e. ["Than-Moi"].

1905a *Plectopylis Villedaryi*, — Dautzenberg & Fischer, Journal de Conchyliologie, 53: 93. ["Dong-Trieu, dans les racines des arbustes qui poussent sur des rochers à ceux de la baie d'Along"].

2013 *Gudeodiscus villedaryi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

Types examined. Haut-Tonkin, NHMUK 1930.9.12.38 (holotype of *villedaryi*, Figure 8C); Tonking, Than-Moi, collection Möllendorff ex Fruhstorfer, SMF 9279 (lectotype of *choanomphala*, Figure 8B); Tonking, Than-Moi, SMF 9276 (paralectotype of *choanomphala*).

Museum material examined. Tonkin, Nja-Ba-Thà, coll. Dosch ex Rolle, SMF 172084/4; Tonkin, Mui-Cho, SMF 172095/4; Tonkin, Than-Moi, coll. Ehrmann ex Fruhstorfer, SMF 150133/2; Tonkin, Muc Cho Nja Ba, coll. Jaeckel, S. H., SMF 207680/3; Tonkin, Mui Aro Nja Ba Thà, HNHM 9576/1; Than-Moi, coll. Letellier, 1949, MNHN-IM-2012-2306/3; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2321/2; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2335/10; Indo-China, coll. Krempf, MNHN-IM-2012-2400/7 juvenile shells; Tonkin, Nju Ba

Thá, coll. Rolle, NHMW 50856/2; Tonkin, coll. Fruhstorfer, NHMW 40848/1; Tonkin, Phu-Ty, coll. Edlauer ex Rolle, NHMW 75000/E/7804/2; "China", coll. Rolle, NHMW 71640/O/12303/1; Tonkin, Moi-Cho-Nja, coll. Rušnov ex Rolle ex Messager, NHMW 92586/2; Tonkin, Than Moi, coll. Edlauer ex Rolle, NHMW 75000/E/7816/3; Tonkin, Nja-Ba-Thá (?), coll. Rušnov ex Blume, NHMW 92584/1; Tonkin, Than-Moi, coll. Rušnov ex Rolle ex Messager, NHMW 92585/1; Tonkin, Than-Moi, coll. Käufel ex Klemm, NHMW 79000/K/17482/2; Tonkin, Cho-Moi, coll. Rolle, NHMW 71640/O/12302/1.

New material examined. Vn10-47A Thái Nguyên Province, ca. 4 km NE of Đình Cả, Phượng Hoàng Cave, 21°46.554'N, 106°07.210'E, leg. Hemmen, Ch. & J., 18.03.2010., PGB/3; **20090520A** Thái Nguyên Province, Võ Nhai District, Phú Thượng Commune, Phượng Hoàng Cave, Mỏ Gà Vill., ca 150 m, 21°46.836'N, 106°07.107'E, leg. Ohara, K., 20.05.2009., OK/15, PGB/4 (anatomically examined, Figures 24, 28G, 32D); **Vn10-128** Lạng Sơn Province, ca. 69 km from Thái Nguyên to Bắc Sơn (right side off road), 21°54.270'N, 106°15.801'E, leg. Hemmen, Ch. & J., 22.10.2010., PGB/1; **2012/58** Thái Nguyên Province, northern edge of Lâu Thượng, 5 km W of Đình Cả, 105 m, 21°44.484'N, 106°01.420'E, leg. Hunyadi, A., 04.06.2012., HA/4; **2011/65** Lạng Sơn Province, Đồng Mỏ 2.5 km towards Văn Quan, right side of the road, 270 m, 21°40.358'N, 106°34.783'E, leg. Hunyadi, A., 10.11.2011., HA/7+2jb, PGB/1; **2011/68** Lạng Sơn Province, Đồng Mỏ 7 km towards Văn Quan, Vạn Linh cross., left side of the road, 370 m, 21°41.158'N, 106°33.588'E, leg. Hunyadi, A., 10.11.2011., HA/1; **2011/76** Lạng Sơn Province, northern edge of Chi Lăng, pass next to the tourist path (N of Đồng Bành) 75 m, 21°34.945'N, 106°30.567'E, leg. Hunyadi, A., 13.11.2011., HA/15+1jb, PGB/2; **2011/79** Lạng Sơn Province, Đồng Mỏ 5.2 km towards Chi Lăng, right side of the road, 40 m, 21°37.215'N, 106°32.538'E, leg. Hunyadi, A., 13.11.2011., HA/3; **2011/102** Thái Nguyên Province, Đình Cả NE 4 km, Phượng Hoàng cave, around the entrance of the cave, 365 m, 21°46.782'N, 106°07.189'E, leg. Hunyadi, A., 13.11.2011., HA/25+2jb, PGB/2 (anatomically examined, Figures 23, 28F, 30A–C, 30F, 35M–O); **2012/38** Lạng Sơn Province, Đồng Mỏ 4–5 km towards Chi Lăng, right side of the old road, 65 m, 21°37.479'N, 106°32.730'E, leg. Hunyadi, A., 25.05.2012., HA/12+1jb; **Vn11-159** Lạng Sơn Province, at km 74.8 on road 1B, Đồng Đăng to Thái Nguyên (8 km S Bắc Sơn), 21°54.543'N, 106°17.298'E, leg. Hemmen, Ch. & J., 02.04.2011., HE/1; **Vn11-163** Lạng Sơn Province, road 242 from Đình Cả to Hữu Lũng, SE Bình Long, 21°38.424'N, 106°11.761'E, leg. Hemmen, Ch. & J., 02.04.2011., HE/9; **Vn11-151** Thái Nguyên Province, ca. 48 km from Thái Nguyên to Bắc Son, near Lâu Thượng (SW Đình Cả), 21°43.522'N, 105°58.662'E, leg. Hemmen, Ch. & J., 29.03.2011., HE/8; **Vn11-161** Lạng Sơn Province, at km 90.5 on road 1B Đồng Đăng to Thái Nguyên, 21°49.656'N, 106°12.636'E, leg. Hemmen, Ch. & J., 02.04.2011., HE/1; **Vn11-152** Lạng Sơn Province, road 1B, ca. 23 km SE Bắc Sơn (between Đình Cả and Bắc Sơn), 21°49.155'N, 106°11.448'E, leg. Hemmen, Ch. & J, 29.03.2011., HE/3.

Diagnosis. Shell medium-sized to large, strongly-built, nearly smooth, with thick apertural lip and an oblique, strong apertural fold (Figure 9J); umbilicus frequently keeled. The anterior parietal lamella is supported by an anteriorly elongated lower plica; an additional, long horizontal plica is present near the lower suture; middle palatal plicae oblique (Figures 13V–Y).

Measurements (in mm): D = 19.5–21.7, H = 11–12.6 (n=4, Vn11-163); D = 15.4–18.4, H = 7.8–8.9 (n=3, Vn11-151); D = 21–23.4, H = 11.3–12.6 (n=3, Vn11-152); D = 15.4–16.5, H = 8.4–9.5 (n=3, 20090520A); D = 16.7–20.6, H = 8.9–9.8 (n=3, Vn10-42); D = 16.1–17.8, H = 7.9–9.2 (n=2, Vn10-44).

Differential diagnosis. See under *Gudeodiscus dautzenbergi* and *Halongella schlumbergeri*.

Intraspecific diversity. The morphology of palatal and parietal plicae and lamellae do not show significant variation. Conversely, shell size, aperture shape, shape of the dorsal side of the shell, spire height and the presence or absence of the periumbilical keel show considerable variation across populations. See also Table 11.

Description of the genitalia. Three specimens were anatomically examined; they were collected at the same locality at different times of the year (20090520A: 20 May, two specimens; 2011/102: 12 November, one specimen). One of the specimens from the 20090520A sample had abnormally developed genitalia. Namely, the penis was "normally" connected to the genital opening, but the vagina was only attached to the atrium area with weak fibres. Nevertheless, the gametolytic sac was filled with fragments of a spermatophore which is an indication of successful mating. An epiphallus was absent and the vas deferens started from the base of the vagina. The other specimen from the 20090520A sample (collected in May) had 18 embryos developed in its uterus, and had no claws between the folds on the inner wall of the penis, whereas the one collected in November was not gravid, but had several claws within the folds inside the penis. The claws had a moderately long base inside the pockets, whereas their hook-like tip was hanging out of the pockets. The SEM images revealed that the base had a granulated surface, probably to provide a better attachment to wall of the pockets, whereas the tip was smooth. Additionally, the specimen from November had parallel, dense, wavy, horizontal folds on the inner wall of the proximal part of the penis, and longitudinal, parallel folds on the distal portion of the penis. The other specimen sampled in May had only a slightly waved proximal part of the longitudinal folds. Other parts of the genitalia did not differ between the two specimens.

The penis is short, pear-shaped internally with pockets standing in a straight row at the distal part of the penis; the epiphallus is much more slender, and is somewhat shorter than the penis; there is no penial caecum, the retractor muscle attaches on the apical part of the penis (at the penis-epiphallus transition); epiphallus approximately as long as the penis, it transforms to vas deferens without obvious boundary; epiphallus internally with parallel folds; vagina long with a well-developed vaginal bulb, it is attached to the body wall with several ligaments; vaginal bulb with thickened wall, internally almost smooth, only with hardly visible longitudinal folds; inner wall of the distal part of the vaginal with low, parallel or converging, serrulate folds (Figure 32D); there is a shorter, thicker gametolytic sac and a longer, more slender diverticulum.

Table 11. Diversity of the periumbilical region within *Gudeodiscus* (*Gudeodiscus*) *villedaryi*.

code	keel
2012/58	absent
2011/65	present
2011/68	present
2011/76	present
2011/79=2012/38	present
2011/102= Vn10-47=20090520A	present
Vn10-128	slight keel
Vn11-159	slight keel
Vn11-151	slight keel
Vn11-152	absent
Vn11-161	slight keel
Vn11-163	present

Radula. See Table 6 and Figures 35M–O.

Distribution (see Figure 40). The species is known from Thái Nguyên and Lạng Sơn provinces.

Remarks. *Gudeodiscus villedaryi* is a very variable species in terms of shell characters. The species is recognised on the basis of the presence of an additional lower plica, which is absent in *G. dautzenbergi*. The latter species might be only a variety of *G. villedaryi* which has lost the lower plica. More information is needed to determine whether the populations assigned to *G. villedaryi* and *G. dautzenbergi* form monophyletic groups. See also under *G. dautzenbergi*.

Subgenus *Veludiscus* Páll-Gergely, subgen. n.

Type species. *Gudeodiscus eroessi* Páll-Gergely & Hunyadi, 2013.

Diagnosis. Shell indistinguishable from those of the subgenus *Gudeodiscus* (*Gudeodiscus*) and the genus *Halongella* gen. n. Anatomy: Epiphallus is slender, cylindrical; retractor muscle inserts on the distal end of the penial caecum, but the whole caecum is covered by additional, fine muscle fibres which insert on the distal end of the penis. Radula: central tooth smaller than the ectocone of the first lateral; mesocone of the first lateral is usually wide, rhomboid. Marginals bi- or tricuspid, with blunt inner cusp and shallow incision between the inner two cusps. See drawings and descriptions of the genital anatomy in Páll-Gergely and Hunyadi (2013) and Páll-Gergely and Asami (2014).

Content. *emigrans* (Möllendorff, 1901), *eroessi* Páll-Gergely & Hunyadi, 2013, *goliath* Páll-Gergely & Hunyadi, 2013(?), *okuboi* Páll-Gergely & Hunyadi, 2013, *pulvinaris* (Gould, 1859).

Etymology. The name *Veludiscus* is composed of two Latin words. Velum (=curtain, sail, covering) refers to the characteristic feature of the genitalia, namely the additional curtain-like muscle covering the penial caecum and the retractor muscle, and discus (=disc) refers to the shape of the shell. The genus is gender masculine.

Remarks. Some conchologically similar species may belong to this subgenus, especially those which inhabit similar geographic regions. Future investigations on the anatomy and radula morphology of *Gudeodiscus* species should clarify the subgeneric status of the taxa with unknown anatomy.

Gudeodiscus (*Veludiscus*) *emigrans* (Möllendorff, 1901)

Diagnosis. A medium-sized to large species with dense, fine riblets; shell flat, callus always, apertural fold usually present. Parietal wall with C-shaped posterior lamella; anterior lamella (if present) slightly S-shaped; if anterior lamella is missing; one lower plica or four parallel plicae are visible in front of the lamella; palatal wall with almost straight, slightly oblique, depressed Z-shaped or Y-shaped plicae (Figures 13A–D).

Differential diagnosis. *Gudeodiscus phlyarius* has stronger apertural fold, a straight anterior parietal lamella (in the Chinese populations assigned to *G. phlyarius werneri* Páll-Gergely, 2013 = synonym of *phlyarius*, sometimes dissolved into small denticles) and usually a somewhat elevated spire. *Gudeodiscus messageri*, *G. hemmeni* sp. n. and *G. anceyi* have two parietal lamellae or several small denticles standing in a line at the position of the first lamella.

General distribution. The three subspecies of *G. emigrans* are known from northern Vietnam and northern Guangxi.

Gudeodiscus (*Veludiscus*) *emigrans emigrans* (Möllendorff, 1901)

Figures 6E, 13A–B

1901 *Plectopylis* (*Sinicola*) *emigrans* Möllendorff, Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft, 33 (5/6): 75, 76. [“Mansongebirge”]

2013 *Gudeodiscus emigrans emigrans*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 12., Figs 24, 44a–b, 58 (map).

Material examined. See Páll-Gergely and Hunyadi (2013).

Diagnosis. Spiral sculpture missing or not conspicuous, parietal wall with one lamella and a short lower parietal plica anterior to the lamella.

Measurements (in mm). D = 17.3, H = 7.5 (holotype).

Differential diagnosis. *Gudeodiscus emigrans emigrans* has weaker spiral sculpture than *G. emigrans quadrilamellatus*, and has only one horizontal parietal plica anterior to the lamella (close to the lower suture), whereas *G. emigrans quadrilamellatus* has four parallel horizontal plicae. The Chinese *G. emigrans otanii* has Y-shaped palatal plicae (these are simple in the nominotypical subspecies and in *G. emigrans quadrilamellatus*).

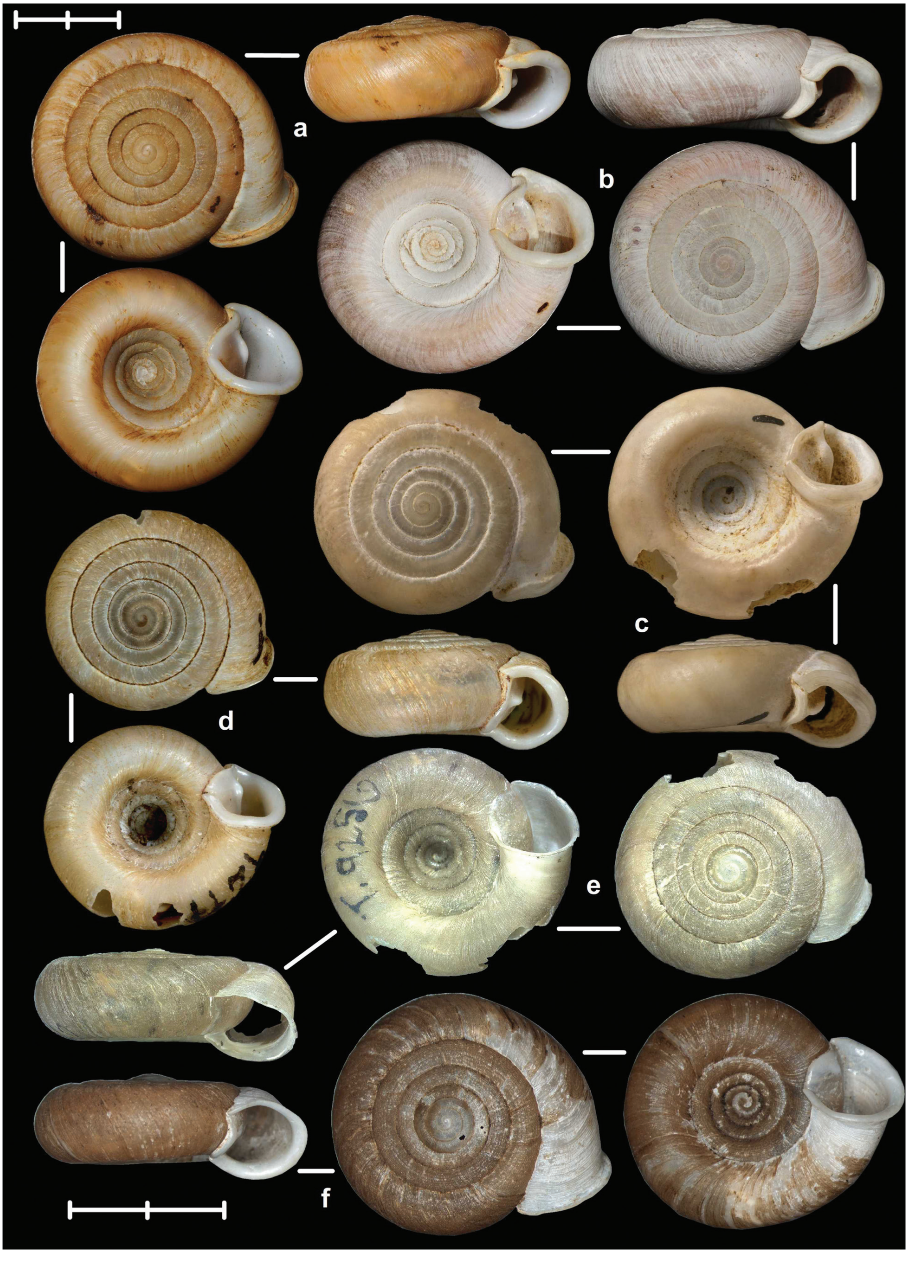

Figure 6. Shells of Vietnamese *Halongella* gen. n. and *Gudeodiscus* species. **A** *Halongella schlumbergeri* (Morlet, 1886), MNHN 24582 (syntype of *Helix* (*Plectopylis*) *schlumbergeri*) **B** *H. schlumbergeri*, MNHN 24580 (syntype of *Plectopylis jovia*) **C** *H. schlumbergeri*, NHMUK 1922.8.29.52 (holotype of *Plectopylis pilsbryana*) **D** *H. schlumbergeri*, SMF 9277 (lectotype of *Plectopylis hirsuta*) **E** *Gudeodiscus* (*Veludiscus*) *emigrans emigrans* (Möllendorff, 1901), SMF 9256 (lectotype) **F** *G.* (*V.*) *emigrans quadrilamellatus* Páll-Gergely, 2013, HNHM 97468 (holotype). Photos E and F were already published in Páll-Gergely and Hunyadi (2013). Photos: T. Deli (**A, B**), H. Taylor (**C**), S. Hof (**D**), E. Neubert (**E**) and B. Páll-Gergely (**F**). Scales represent 10 mm; upper scale belongs to **A–B**, lower scale belongs to **C–F**.

Figure 7. Shells of Vietnamese *Gudeodiscus* and *Halongella* gen. n. species. **A** *Gudeodiscus* (*Gudeodiscus*?) *francoisi* (Fischer, 1898), MNHN 24601 (holotype of *Plectopylis bavayi*) **B** *G.* (*G.*?) *francoisi*, MNHN 9945 (holotype of *Plectopylis francoisi*) **C** *G.* (*G.*?) *francoisi*, NHMUK 1922.8.29.51 (holotype of *Plectopylis lepida*) **D** *Halongella fruhstorferi* (Möllendorff, 1901), SMF 9258 (lectotype) **E** *G.* (*G.*) *giardi giardi* (Fischer, 1898), MNHN IM-2010-12120 (syntype of *Plectopylis congesta*) **F** *G.* (*G.*) *giardi giardi*, NHMUK 1922.8.29.49 (syntype of *Plectopylis congesta*). Photos: T. Deli (**A, B, E**), H. Taylor (**C, F**) and E. Neubert (**D**). Scale represents 20 mm.

Figure 8. Shells of Vietnamese *Gudeodiscus* and *Halongella* gen. n. species. **A** *Gudeodiscus* (*Gudeodiscus*) *giardi giardi* (Fischer, 1898), MNHN 9946 (syntype of *Plectopylis giardi*) **B** *G.* (*G.*) *villedaryi* (Ancey, 1888), SMF 9279 (lectotype of *Plectopylis choanomphala*) **C** *G.* (*G.*) *villedaryi*, NHMUK 1930.9.12.38 (holotype of *Plectopylis villedaryi*) **D** *G.* (*G.*) *villedaryi*, Vn11-152, coll PGB **E** *G.* (*G.*) *dautzenbergi* (Gude, 1901), MNHN 24603 (holotype) **F** *G.* (*G.*) *dautzenbergi*, MNHN 24602 (holotype of *Plectopylis persimilis*). Photos: T. Deli (**A, E, F**), S. Hof (**B**), H. Taylor (**C**) and B. Páll-Gergely (**D**). Scale represents 20 mm.

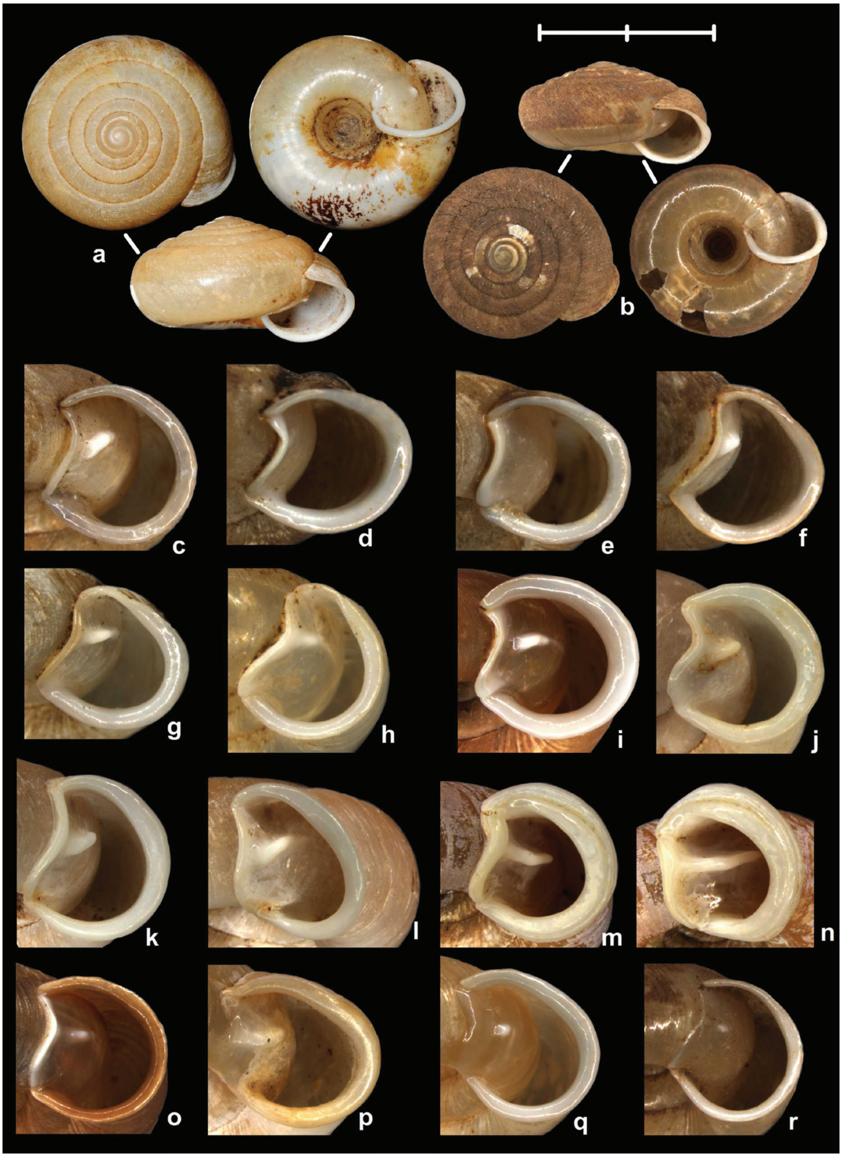

Figure 9. Shells (**A–B**) and apertural views (**C–R**) of Vietnamese *Gudeodiscus*, *Sicradiscus* and *Halongella* gen. n. species. **A** *Gudeodiscus* (*Gudeodiscus*?) *suprafilaris* (Gude, 1908), MNHN 24586 (holotype?) **B** *G.* (*G.*?) *suprafilaris*, 2011/81 **C** *G.* (*G.*) *phlyarius* (Mabille, 1887), Vn11-156 **D** *G.* (*G.*) *phlyarius* (Mabille, 1887) (typical "*anterides*/*gouldingi*"), MNHN-IM-2012-2164 **E** *G.* (*G.*) *messageri messageri* (Gude, 1909), MNHN-IM-2012-2215 **F** *G.* (*G.*?) *hemmeni* Páll-Gergely & Hunyadi, sp. n., Vn10-103A **G** *G.* (*G.*?) *anceyi* (Gude, 1901), GS22 **H** *Sicradiscus mansuyi* (Gude, 1908), 20081116C **I** *G.* (*G.*) *giardi giardi* (Fischer, 1898), 2011/81 **J** *G.* (*G.*) *villedaryi* (Ancey, 1888), Vn11-151 **K–L** *G.* (*G.*) *dautzenbergi* (Gude, 1901), Vn10-44 **M–N** *Halongella schlumbergeri* (Morlet, 1886), MAA3 **O** *H. fruhstorferi* (Möllendorff, 1901), Vn11-171 **P** *G.* (*G.*) *fischeri* (Gude, 1901), Vn10-120 **Q** *G.* (*G.*) *fischeri* (Gude, 1901), 20090515C **R** *G.* (*G.*?) *suprafilaris* (Gude, 1908), 2011/81. All photos by B. Páll-Gergely except for Figure 9A (T. Deli). Scale represents 10 mm and refers to **A** and **B**.

Moreover, some specimens of *G. emigrans otanii* have two vertical lamellae (see Páll-Gergely and Asami 2014).

Intrasubspecific diversity. Very few shells are known from museum collections. The subspecies is easily recognisable, but more material is needed to understand the intrasubspecific diversity.

Distribution. *Plectopylis* (*Sinicola*) *emigrans* was described from the "Manson-Gebirge" = "Mau Son Mts, about 30 km E of Lang Son" (Schileyko 2011) (see Figure 39).

***Gudeodiscus* (*Veludiscus*) *emigrans quadrilamellatus* Páll-Gergely, 2013**

Figures 6F, 13C–D

1901a *Plectopylis emigrans* Gude, Journal de Conchyliologie, 49: 206–208. Plate 6., Figs 5a–c. ["Bac Kan, secteur de Nac Ri, Baie d'Along"].

2013 *Gudeodiscus emigrans quadrilamellatus* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 15–17., Figs 27, 45a–b, 58 (map).

Material examined. Samples not mentioned in Páll-Gergely and Hunyadi (2013) are the following: Hạ Long Bay, leg. Messager, MNHN-IM-2012-2320/1; Indochine, leg. Messager, MNHN-IM-2012-2455/2; Tonkin, coll. Letellier 1949, MNHN-IM-2012-2448/1.

Diagnosis. Spiral sculpture conspicuous, parietal wall with one lamella and four parallel horizontal plicae in front of the single lamella.

Measurements (in mm): D = 17.7–18.6, H = 7.1–7.6 (n=3, sample from the type locality).

Differential diagnosis. See under *Gudeodiscus emigrans emigrans*.

Intrasubpecific diversity. Low; shell characters are stable. The subspecies is easily recognisable and can be separated from other Vietnamese and Chinese taxa without problems.

Distribution (see Figure 42): *Gudeodiscus emigrans quadrilamellatus* is known from Bắc Kạn and Tuyên Quang Provinces. Museum samples are labelled from Tam Đảo, on the border region of Thái Nguyên and Vĩnh Phúc Provinces (Au Nord de Ha Noi, Tam Dao, MNHN-IM-2012-2123/3). Records from the Hạ Long area (e.g. Gude 1901a) are probably incorrect (see also Páll-Gergely and Hunyadi 2013).

Genus *Halongella* Páll-Gergely, gen. n.

http://zoobank.org/F77AFB6D-87D8-4F33-B3F7-0F0F859A783F

Type species. *Helix* (*Plectopylis*) *Schlumbergeri* Morlet, 1886.

Diagnosis. Shells do not differ from those of *Gudeodiscus*; small to very large, body whorl rounded, callus and apertural fold; Parietal wall with two lamellae or the ante-

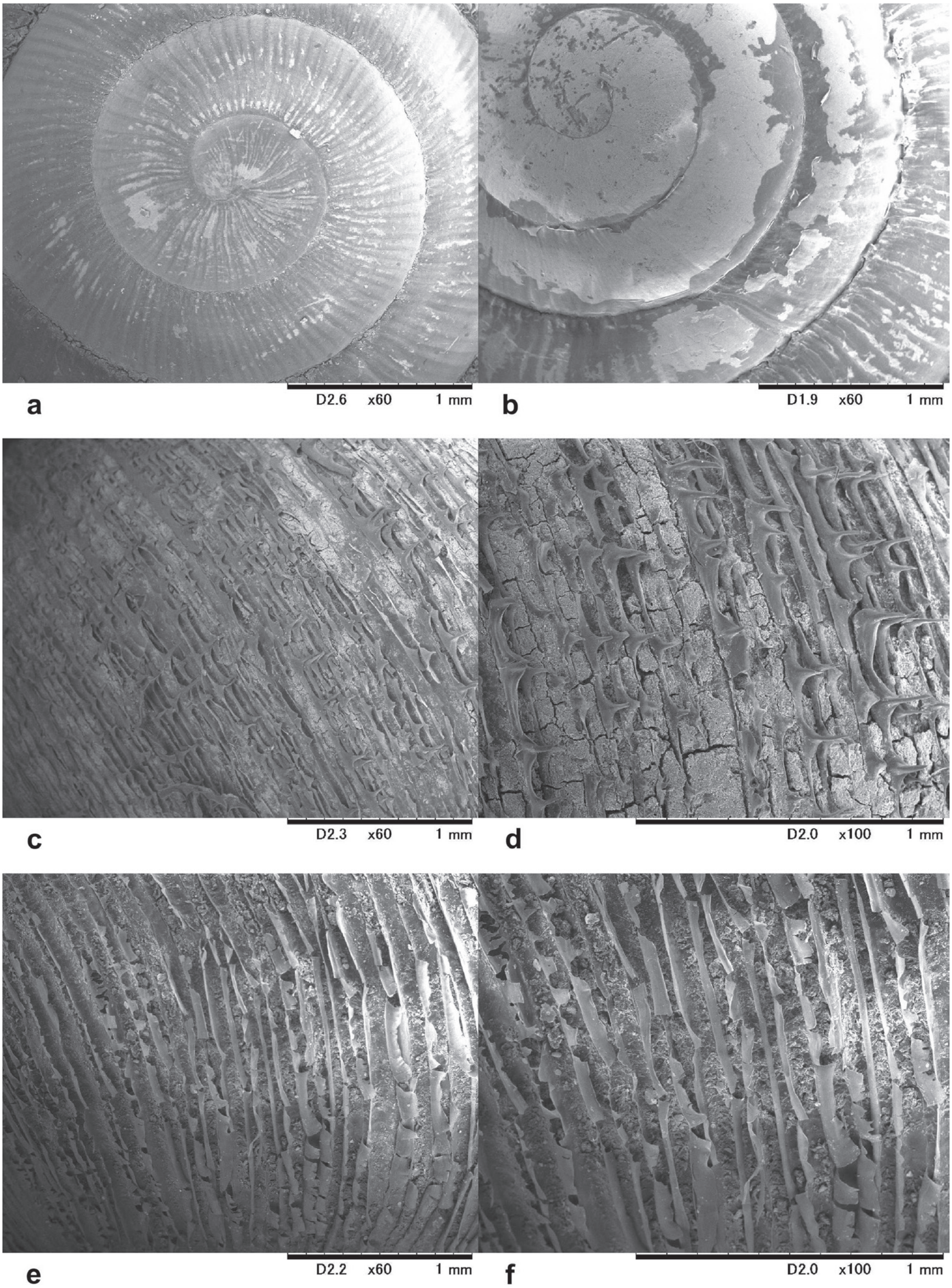

Figure 10. SEM images of *Gudeodiscus* shells. **A** protoconch of *Gudeodiscus* (*Gudeodiscus*) *messageri raheemi* Páll-Gergely & Hunyadi, ssp. n., Vn12-104, coll. HE **B** protoconch of *G.* (*G.*) *villedaryi* (Ancey, 1888), Vn11-163, coll. HE **C–D** sculpture of *G.* (*G.*) *phlyarius* (Mabille, 1887), Vn10-56, coll. HE **E–F** sculpture of *G.* (*G.*) *phlyarius* (Mabille, 1887) (typical *fallax* specimen), Vn11-187, coll HE. Images: B. Páll-Gergely.

rior one is reduced or absent; parietal side with straight, slightly curved, or depressed Z-shaped plicae.

Penial caecum absent. Penis internally with longitudinal, parallel folds, with tiny, flat, T-shaped calcareous granules between the folds, all along the penis; there are no determined "pockets" for the granules at the apical part of the penis. Epiphallus internally with longitudinal folds having several perpendicular projections which overlap with those of the neighbouring fold. Radula similar to *Gudeodiscus* (*Veludiscus*) subgen. n. by the smaller central tooth than the ectocone of the first laterals and the marginals which are bicuspid or tricuspid with blunt innermost cups and shallow incision between the two inner cusps.

Differential diagnosis. *Sinicola* species have a keeled body whorl, whereas it is rounded in *Halongella* gen. n. Moreover, all *Sinicola* species have a penial caecum, a central tooth which is as large as or larger than the ectocone of the first laterals and clearly tricuspid marginals with deep incision between the innermost two, sharp cusps. The same radular morphology has been observed in *Sicradiscus* species. Additionally, "eastern" *Sicradiscus* species possess keeled shells, whereas the rounded shelled "western" species of the genus have determined pockets on the inner penial wall, similar to that of *Gudeodiscus*. For comparison with *Gudeodiscus*, see there.

Included taxa. *fruhstorferi* Möllendorff, 1901 and *schlumbergeri* Morlet, 1886.

Etymology. This generic name derives from the name of the Halong Bay, where both species occur. The genus is gender feminine.

Remarks. Calcareous granules of complicated shape have been found in the vagina of *Halongella schlumbergeri*, and some granules not having characteristic shapes have been found in the vaginal lumen of *H. fruhstorferi*. The taxonomic value of these granules are unknown. No granules of characteristic shape have been found in the vaginas of *Gudeodiscus* species, therefore this can be a synapomorphy of *Halongella* gen. n.

Halongella fruhstorferi **(Möllendorff, 1901)**

Figures 7D, 9O, 14O–R, 25, 29C, 29I, 32A–B, 36A–C

1901 *Plectopylis* (*Sinicola*) *fruhstorferi* Möllendorff, Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft, 33(5/6): 114–115. [no locality specified].

1901c *Plectopylis* (*Sinicola*) *fruhstorferi*, — Gude, Journal of Malacology, 8: 112–113., Figs 2a–e. ["Kebao"].

1915 *Plectopylis fruhstorferi*, — Gude, Records of the Indian Museum, 8: 513.

2013 *Gudeodiscus fruhstorferi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

Types examined. Tonkin, Kebao, collection Möllendorff ex Fruhstorfer 128, SMF 9258 (lectotype); Tonkin, Kebao, collection Möllendorff ex Fruhstorfer 128, SMF 9259 (paralectotype).

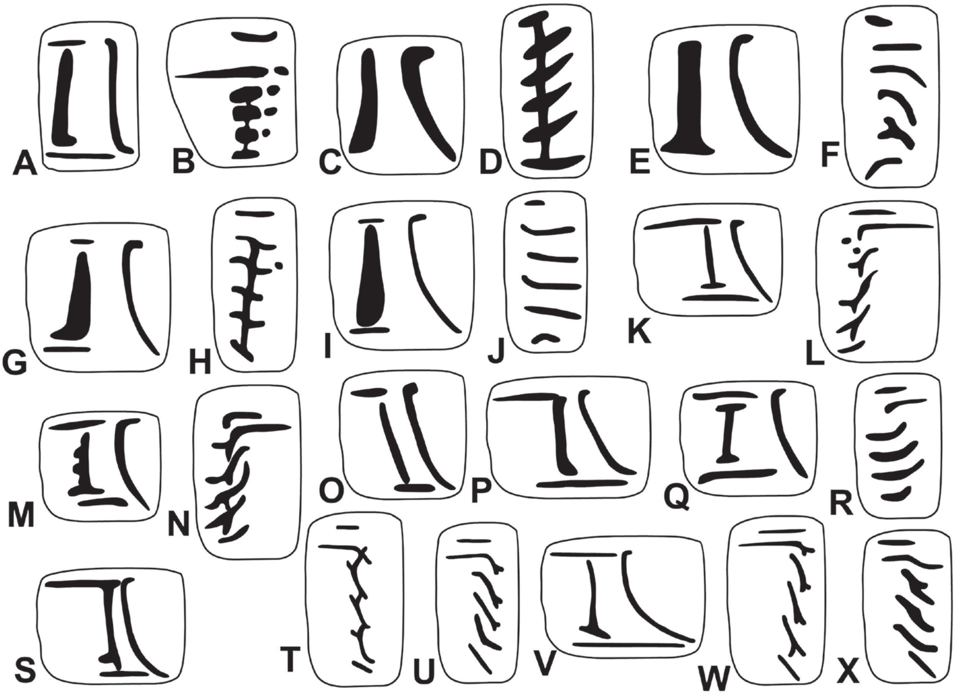

Figure 11. Parietal (**A, C, E, G, I, K, M, O–Q, S, V**) and palatal (**B, D, F, H, J, L, N, R, T–U, W–X**) plicae and lamellae of *Sicradiscus* and *Gudeodiscus* species. **A–B** *Sicradiscus mansuyi* (Gude, 1908), 20081116C (two different specimens) **C–F** *Gudeodiscus* (*Gudeodiscus*) *anceyi* (Gude, 1901) **C–D** figures in Gude (1901a) **E** MNHN-IM-2012-2263, **F** GS22 **G–J** *G.* (*G.*?) *hemmeni* Páll-Gergely & Hunyadi, sp. n. **G–H** 2012/62, spec.1 **I–J** 2012/62, spec.2 **K–P** *G.* (*G.*) *phlyarius* (Mabille, 1887) (typical *gouldingi* and *anterides* shells) **K–L** *Plectopylis gouldingi* (after Gude 1909) **M–N** *Plectopylis anterides* (after Gude 1909) **O–P** MNHN-IM-2012-2153 **Q–X** *G.* (*G.*) *phlyarius* (typical *fallax* and *fallax* var. *major* shells) **Q–R** *Plectopylis fallax* (after Gude 1909) **S** MNHN-IM-2012-2157 **T–U** MNHN-IM-2012-2132 (2 different specimens) **V–W** MNHN-IM-2012-2155/6 ("var. *major*", two different specimens), **X** Vn11-187. Inner view: **D, L, N, R**; Outer view: **B, F, H, J, T, U, W, X**.

Museum material examined. Tonkin, Kebao (Insel), SMF 150081/2; Kebao, leg. Fruhstorfer, 29.10.1900, RBINS/2; Kebao, coll. Rolle, NHMUK 20110239/2; Kebao, NHMUK 1901.12.23.41–43/3; Tonkin, NHMUK 1916.3.16.9/1.

New material examined. Vn11-171 Quảng Ninh Province, Vân Đồn Island (NE Cẩm Phả), Cái Rồng village, 21°3.560'N, 107°25.551'E, leg. Hemmen, Ch. & J., 14.08.2011., HE/23, HA/1, PGB/3 (anatomically examined, Figures 25, 29C, 29I, 32A–B, 36A–C).

Diagnosis. Shell small, solid, thin-walled, almost flat and smooth, with weak apertural lip and sometimes a small apertural denticle (Figure 9O). Parietal wall with one parietal lamella with two short horizontal plicae anteriorly, one above and one below; palatal plicae short, oblique, depressed Z-shaped (Figures 14O–R).

Measurements (in mm). D = 13.1–13.4, H = 5.8–6 (n=2, Vn11-171).

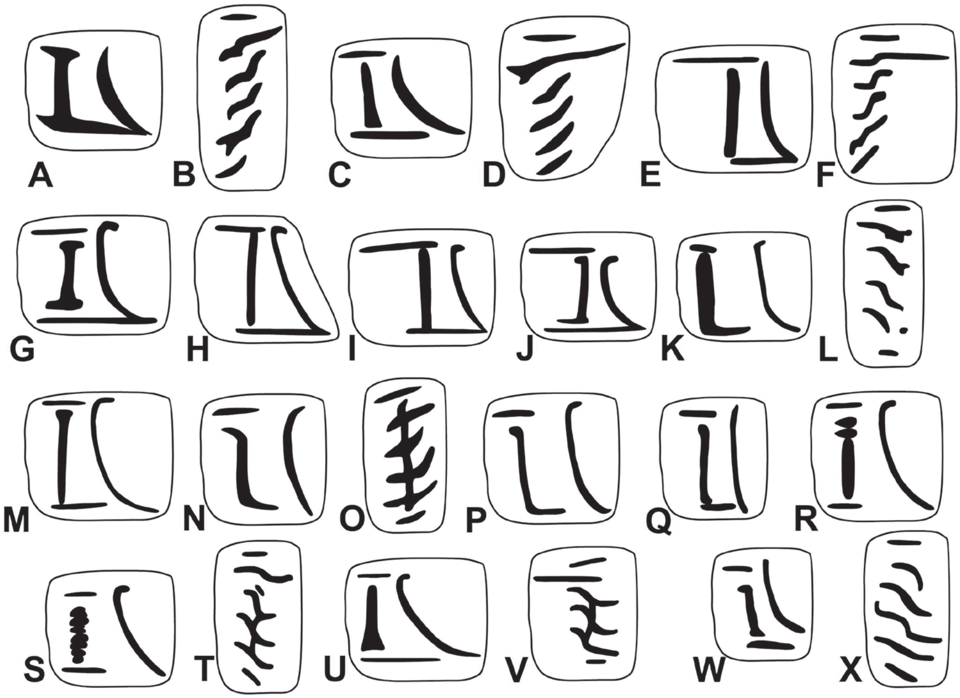

Figure 12. Parietal (**A, C, E, G–K, M, N, P–S, U, W**) and palatal (**B, D, F, L, P, T, V, X**) plicae and lamellae of *Gudeodiscus* species. **A–M** *Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887) **A–B** *Plectopylis phlyaria* (after Gude 1901c) **C–D** *Plectopylis moellendorffi* (after Gude 1901c) **E–F** Vn10-49, **G** Vn09-24 **H** Vn10-56, **I** Vn9-16, spec.1 **J** Vn9-16, spec.2 **K–M** *Plectopylis verecunda*, MNHN 2012-2177 (3 different specimens) **N–Q** *G.* (*G.*) *messageri messageri* (Gude, 1909) **N–O** *Plectopylis messageri* (after Gude 1909) **P** MNHN-IM-2012-2162, **Q** MNHN-IM-2012-2165 **R–V** *G.* (*G.*) *messageri raheemi* ssp. n, **R** 20071116C, spec.1. **S–T** 20071116C, spec.2. **U–V** 20080509C **W–X** Vn10-104B. Inner views: **B, D, F, O**; Outer views: **L, T, V, X**.

Differential diagnosis. *Halongella fruhstorferi* and *H. schlumbergeri* are congeneric based on similarity of genital morphology. *Halongella fruhstorferi* is smaller than *H. schlumbergeri*, having a more fragile, lighter shell and weaker apertural lip and apertural fold. In shape, *H. fruhstorferi* resembles *Gudeodiscus fischeri*. However, *H. fruhstorferi* has a relatively smaller aperture, weaker sculpture (rather irregular growth lines instead of regular ribs) and an anterior lamella is absent. *Gudeodiscus phlyarius* and the similar species (*G. anceyi*, *G. hemmeni* sp. n., *G. messageri*) have a well-developed anterior lamella or denticles at the position of the anterior lamella.

Intraspecific diversity. The species is known from a very small area, and only few specimens are known. The intraspecific diversity is low.

Description of the genitalia. One specimen was examined anatomically. Locality: Quảng Ninh Province, Vân Đồn Island (NE Cẩm Phả), Cái Rồng village, 21°3.560'N, 107°25.551'E, leg. Hemmen, Ch. & J., 14.08.2011. (Figures 25, 29C, 29I, 32A–B).

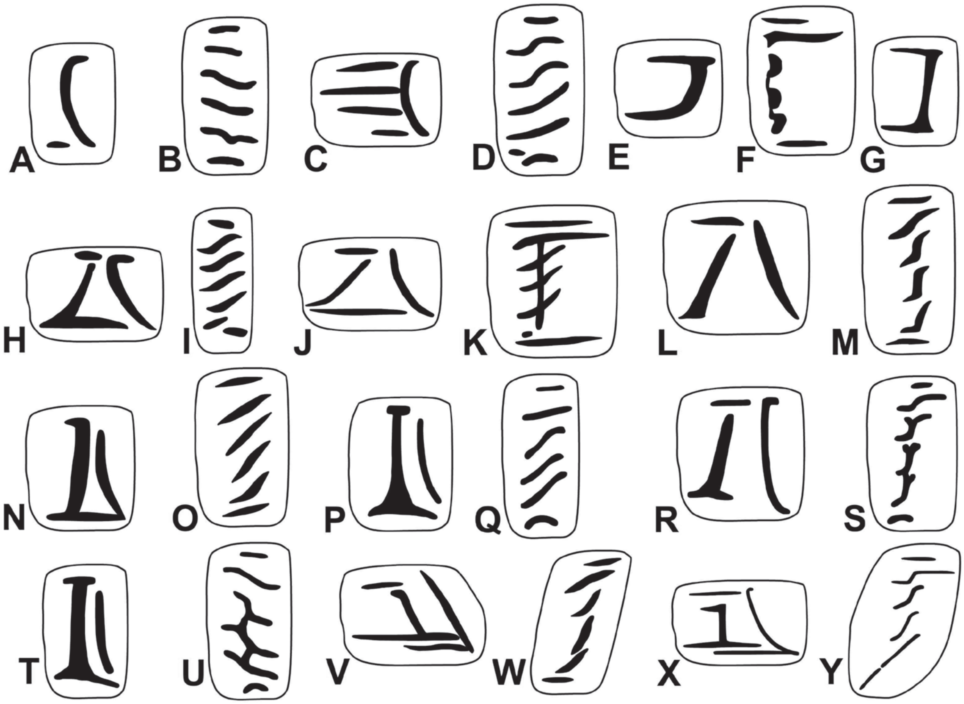

Figure 13. Parietal (**A, C, E, F, H, J, L, N, P, R, T, V,** X) and palatal (**B, D, G, I, K, M, O, Q, S, U, W, Y**) plicae and lamellae of *Gudeodiscus* species. **A–B** *Gudeodiscus* (*Veludiscus*) *emigrans emigrans* (Möllendorff, 1901), holotype (after Páll-Gergely and Hunyadi 2013) **C–D** *G.* (*V.*) *emigrans quadrilamellatus* Páll-Gergely, 2013 (after Páll-Gergely and Hunyadi 2013) **E–K** *G.* (*G.?*) *francoisi* (Fischer, 1898) **E–F** holotype of *Plectopylis lepida* Gude, 1901 (after Gude 1901b), **G** MNHN-IM-2012-2311 **H–I** holotype of *Plectopylis bavayi* Gude, 1901 (after Gude 1901a) **J–K** *Plectopylis francoisi* (after Gude 1899b) **L–U** *G.* (*G.*) *giardi giardi* (Fischer, 1898) **L** *Plectopylis giardi* (after Gude 1899a) **M** *Plectopylis giardi* (after Gude 1899b) **N–O** *Plectopylis congesta* Gude, 1899 (after Gude 1899a); **P–Q** Vn10-69 **R–S** Vn10-59 **T–U** 2011/85 **V–Y** *G.* (*G.*) *villedaryi* (Ancey, 1888) **V–W** holotype of *Plectopylis* (*Endoplon*) *choanomphala* Möllendorff, 1901 (after Gude 1901c) **X–Y** Vn10-47A. Inner views: **D, F, I, K, M, O, Q, S, W, Y**; Outer views: **B, U**.

Penis relatively long, spindle-shaped, inner wall with several (at least 20) parallel running folds (Figure 29C); between the folds flat and very fine calcareous granules were found; epiphallus shorter than the penis, its inner wall with six parallel folds; on the distal portion of the epiphallus the longitudinal folds have several perpendicular projections which overlap with those of the neighbouring fold (Figure 29I); penial caecum absent, the retractor muscle inserts on the penis-epiphallus transition. Vagina long, with a relatively well-developed vaginal bulb; it is attached to the body wall by connective tissue; inner wall of the vagina with at least 16, more or less parallel folds; a few irregularly shaped calcareous granules have been found between the folds (Figure 32A–B); stalk of gametolytic sac longer with thickened gametolytic sac, diverticulum slimmer without conspicuous distal thickening. There were two developing embryos in the uterus. The embryos were surrounded with egg capsules which had several calcareous granules.

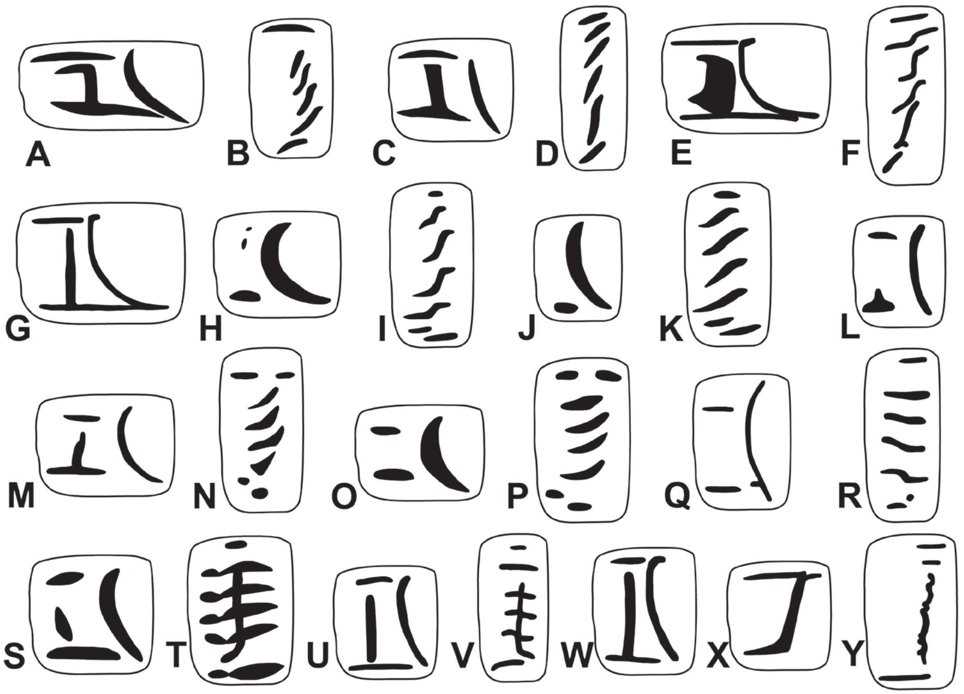

Figure 14. Parietal (**A, C, E, G, H, J, L, M, O, Q, S, U, W, X**) and palatal (**B, D, F, I, K, N, P, R, T, V, Y**) plicae and lamellae of *Gudeodiscus* and *Halongella* gen. n. species. **A–G** *Gudeodiscus* (*Gudeodiscus*) *dautzenbergi* (Gude, 1901) **A–B** *Plectopylis dautzenbergi* (after Gude 1901a) **C–D** *Plectopylis persimilis* Gude, 1901 (after Gude 1901a) **E–F** Vn10-44, **G** Vn10-44 **H–N** *Halongella schlumbergeri* (Morlet, 1886) **H–I** *Plectopylis jovia* (after Gude 1901b) **J–K** *Plectopylis schlumbergeri* (after Gude 1901b) **L** MNHN-IM-2012-2481 **M–N** holotype of *Plectopylis hirsuta* Möllendorff, 1901 (after Gude 1901c) **O–R** *H. fruhstorferi* (Möllendorff, 1901) **O–P** after Gude (1901c) **Q–R** Vn11-171 **S–Y** *G.* (*G.*?) *suprafilaris* (Gude, 1908) **S–T** after Gude (1908) **U–V** 2011/81, spec.1. **W** 2011/81, spec.2. **X–Y** Vn10-125. Inner views: **B, D, F, I, K, N, P, T**; Outer views: **R, V, Y**.

Radula. See Table 6 and Figures 36A–C.

Distribution (see Figure 40): The species is known only from Kebao Island (Hạ Long Bay area).

Halongella schlumbergeri (Morlet, 1886a)

Figures 6A–D, 9M–N, 14H–N, 26, 29A–B, 29H, 30G–I, 33A–G, 36D–F, 45B

1886a *Helix* (*Plectopylis*) *Schlumbergeri* Morlet, Journal de Conchyliologie, 34: 259, 272–274., Plate 12., Figs 2a–c. [“Baie d’Along et montagne de l’Éléphant”].

1886b *Helix* (*Plectopylis*) *Schlumbergeri* Morlet, Diagnoses de mollusques terrestres et fluviatiles du Tonkin. 1–2.

1887b *Plectopylis Schlumbergeri*, — Mabille, Bulletin de le Société Malacologique de France, 4: 101–102.

1887b *Plectopylis jovia* Mabille, **syn. n.**, Bulletin de le Société Malacologique de France, 4: 99–100. ["Circa locum dictum Halong"].
1887 *Helix schlumbergeri*, — Tryon, Manual of Conchology. 2 (3): 166, Plate 36., Figs 25–28.
1888 *Plectopylis Schlumbergeri*, — Ancey, Le Naturaliste, 2(10): 72.
1893 *Plectopylis jovia*, — Pilsbry, Manual of Conchology..., 2 (8): 156–157.
1893 *Plectopylis villedaryi*, — Pilsbry, Manual of Conchology..., 2 (8): 158., Plate 43., Figs 36–39.
1894 *Plectopylis jovia*, — Pilsbry, Manual of Conchology...: 146., Plate 40., Figs 1–4.
1897b *Plectopylis schlumbergeri*, — Gude, Science Gossip, 4: 138., Figs 58a–b. ["Halong Bay and Elephant Mountain, Tonkin"].
1897b *Plectopylis jovia*, — Gude, Science Gossip, 4: 138–139., Figs 59a–b. ["Halong"].
1899a *Plectopylis schlumbergeri*, — Gude, Science Gossip, 5: 332.
1899a *Plectopylis jovia*, — Gude, Science Gossip, 5: 332.
1899c *Plectopylis* (*Endoplon*) *schlumbergeri*, — Gude, Science Gossip, 4: 148.
1899c *Plectopylis* (*Endoplon*) *jovia*, — Gude, Science Gossip, 4: 148.
1899d *Plectopylis* (*Endoplon*) *schlumbergeri*, — Gude, Science Gossip, 6: 175.
1899d *Plectopylis* (*Endoplon*) *jovia*, — Gude, Science Gossip, 6: 175.
1901 *Plectopylis* (*Endoplon*) *hirsuta* Möllendorff, **syn. n.**, Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft, 33 (5/6): 114–115. ["in insula Bah-mun"].
1901a *Plectopylis Schlumbergeri*, — Gude, Journal de Conchyliologie, 49: 199.
1901a *Plectopylis Villedaryi*, — Gude, Journal de Conchyliologie, 49: 212. ["Llots de la baie d'Along"].
1901b *Plectopylis jovia*, — Gude, Journal of Malacology, 8: 47–48., Figs 1a–b.
1901b *Plectopylis schlumbergeri*, — Gude, Journal of Malacology, 8: 47–48., Figs 2a–b.
1901b *Plectopylis villedaryi*, — Gude, Journal of Malacology, 8: 47–48., Figs 3a–b.
1901c *Plectopylis pilsbryana* Gude, **syn. n.**, Journal of Malacology, 8: 110., ["Lang-Son, Bac-Ninh (Vathelet). Isles in Along Bay (Messager). Tonkin (Fruhstorfer)"].
1901c *Plectopylis* (*Endoplon*) *hirsuta*, — Gude, Journal of Malacology, 8: 111–112., Figs 1a–f. ["Island Bah-Mung"].
1901c *Plectopylis* (*Endoplon*) *jovia*, — Gude, Journal of Malacology, 8: 111–112., Figs 1a–f.
1905a *Plectopylis Schlumbergeri*, — Dautzenberg & Fischer, Journal de Conchyliologie, 53: 93.
1905a *Plectopylis jovia*, — Dautzenberg & Fischer, Journal de Conchyliologie, 53: 93.
1905a *Plectopylis Villedaryi*, — Dautzenberg & Fischer, Journal de Conchyliologie, 53: 93.
2013 *Gudeodiscus schlumbergeri*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 8.
2013 *Gudeodiscus pilsbryana*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.
2013 *Gudeodiscus jovius*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.
2013 *Gudeodiscus hirsutus*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 8.

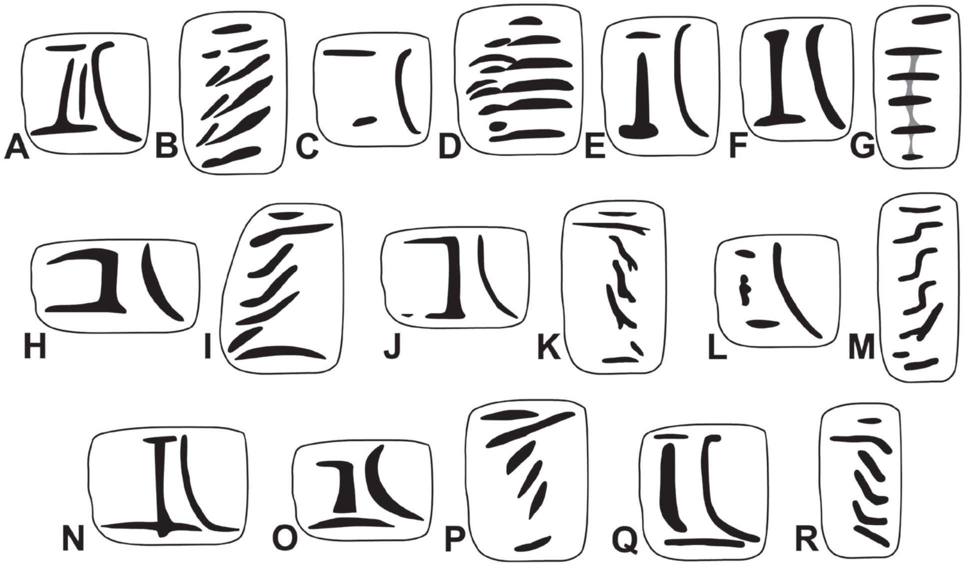

Figure 15. Parietal (**A, C, E, F, H, J, L, N, O, Q**) and palatal (**B, D, G, I, K, M, P, R**) plicae and lamellae of *Gudeodiscus* species. **A–D** *Gudeodiscus* (*Gudeodiscus*) *infralevis* (Gude, 1908) **A–B** holotype of *Plectopylis infralevis* (after Gude 1908) **C–D** Holotype of *Plectopylis soror* (after Gude 1908) **E–G** *G.* (*G.*?) *cyrtochilus* (Gude, 1909) **E–F** MNHN-IM-2012-2251 (two different specimens) **G** 2012/47 **H–N** *G.* (*G.*) *fischeri* (Gude, 1901) **H–I** *Plectopylis fischeri* (after Gude 1901a) **J–K** 20090515C **L–M** Vn10-120 **N** MNHN-IM-2012-2241 **O–R** *G.* (*G.*) *fischeri* (Gude, 1901) (identical with the holotype of *tenuis*) **O–P** after Gude (1901a) **Q–R** Vn10-28A (two different specimens). Inner views: **B, D, I, M, P**; Outer views: **G, K, R**.

Types examined. Llots de la Baie d'Along, leg. Messager (n. 23.), MNHN IM-2010-12119. (cited in Journal de Conchyliologie, 49: 212. as *villedaryi*); Tonkin, Halong, leg. l'Abbé Vathelet, MNHN 24580 (one adult and one juvenile syntypes of *jovia*, Figure 6B); Tonkin, NHMUK 1922.8.29.52 (holotype of *pilsbryana*, Figure 6C); Tonkin, MNHN 24582 (2 syntypes of *schlumbergeri*, Figure 6A); Tonkin, Bah-Mun, coll. Möllendorff ex Fruhstorfer, SMF 9277 (lectotype of *hirsuta*, Figure 6D); same data, SMF 9278 (2 paralectotypes of *hirsuta*).

Museum material examined. Tonkin, That-Khé, coll. Dosch ex Rolle ex Messager, SMF 341737/2; Tonkin, ex Fruhstorfer, SMF 150132/2; Tonkin, Tafel Insel, ex Fruhstorfer, H. 126, SMF 150131/2; Tonkin, Isle de la Table, coll. Ehrmann ex Webb, W. F., SMF 150130/3; Tonkin, Isle de la Table, coll. Ehrmann ex Webb, W. F., SMF 150124/1; Tonkin, coll. Ehrmann ex Fruhstorfer, H., SMF 150123/1; Tonkin, rochers de Kuy-Dong-Kay, coll. Jaeckel, S. H., SMF 207677/2; Tonkin, Isle de la Table, SMF 207678/1; Tonkin, rochers de Nuy-Dong-Nay, coll. Schlickum 3969 ex Staid (?), SMF 277560/2; Tonkin, Than-Moi, coll. Jaeckel, S. H., SMF 207670/4; Tonkin, rochers de Nuy-Dong-Nuy, coll. Pfeiffer, K. L. ex Sundler, October 1940, SMF 102825/2; Tonkin, Ile de la Table, Baie d'Along, SMF 294868/2; Tonkin, coll. Dosch ex Rolle, SMF 172096/2; Tonkin, Ile de la Table, coll. Dosch ex Rolle ex Webb, SMF 172094/2; Tonkin, Ile des Merveilles, coll. Möllendorff ex

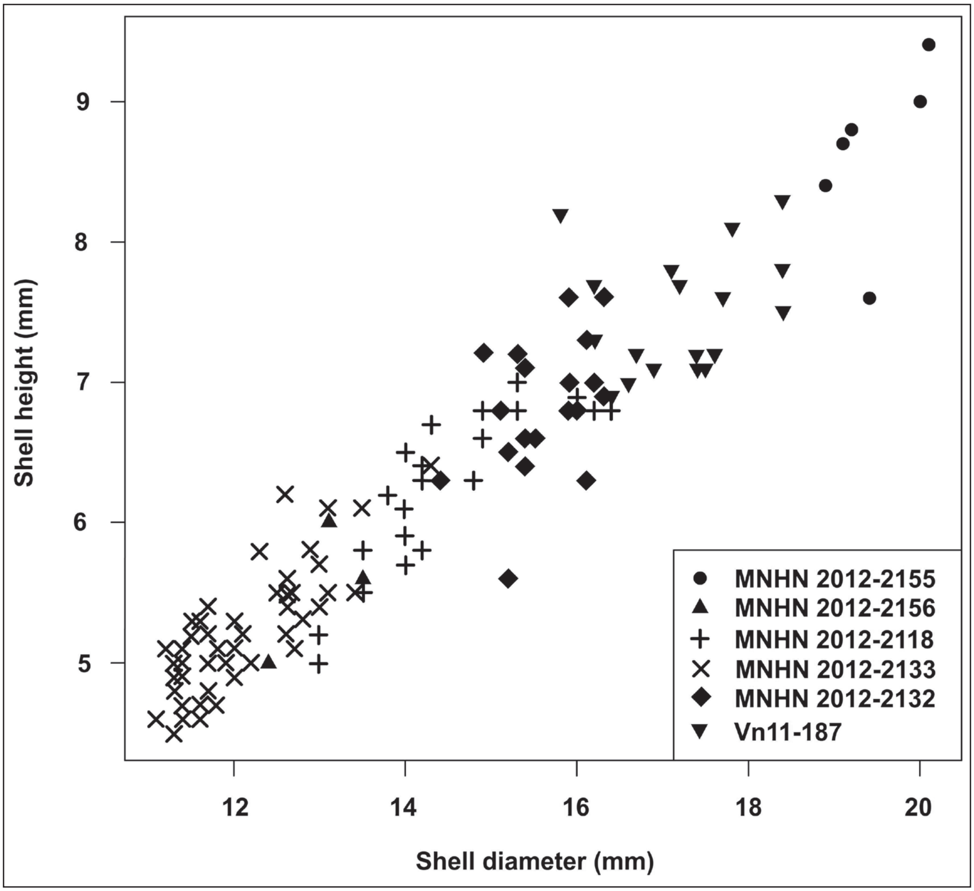

Figure 16. Plot of shell height against shell width (diameter) for 122 adults of *Plectopylis* cf. *anterides*/*gouldingi* (MNHN 2012-2133, MNHN 2012-2156, partly MNHN 2012-2218), *Plectopylis* cf. *fallax* (Vn11-187, MNHN 2012-2132, partly MNHN 2012-2218) and *Plectopylis* cf. *fallax* var. *major* (MNHN 2012-2155) from northern Vietnam. Samples MNHN 2012-2155 and MNHN 2012-2156 originally belonged to the same sample.

Fruhstorfer 130, SMF 150129/2; Tonkin, Hai-fong, coll. Möllendorff ex Fruhstrofer, SMF 150128/1; Hongay, leg. Drimmer, 09.11.1986. ex Kovács, Gy., HNHM 67079/2; Hongay, leg. Drimmer, 09.11.1986., HNHM 78324/4; Nuy Dong Nay, leg. Drimmer, HNHM 67068/1; Tonkin: Roches de Nuy-Dong-Nay HNHM 37877/2; Tonkin, coll. Mansuy, MNHN-IM-2012-2260/4; Tonkin, coll. Sayer 1969, MNHN-IM-2012-2261/1; Tonkin, leg. abbe Wathelet, MNHN-IM-2012-2262/3; Baie d'Along, Ile de le Table, coll. Lavezzari ex Bernays, MNHN-IM-2012-2264/3; Tonkin, coll. Balansa 1887, MNHN-IM-2012-2269/4; Baie d'Halong, excoll. labo. de Géologie de la Sorbonne (entrée 1952), MNHN-IM-2012-2271/2; Baie d'Halong, coll. Staadt, 1969, MNHN-IM-2012-2280/1 juvenile shell; Baie d'Along, Ile de la Table, MNHN-IM-2012-2289/3; Tonkin, coll. Staadt 1969, MNHN-

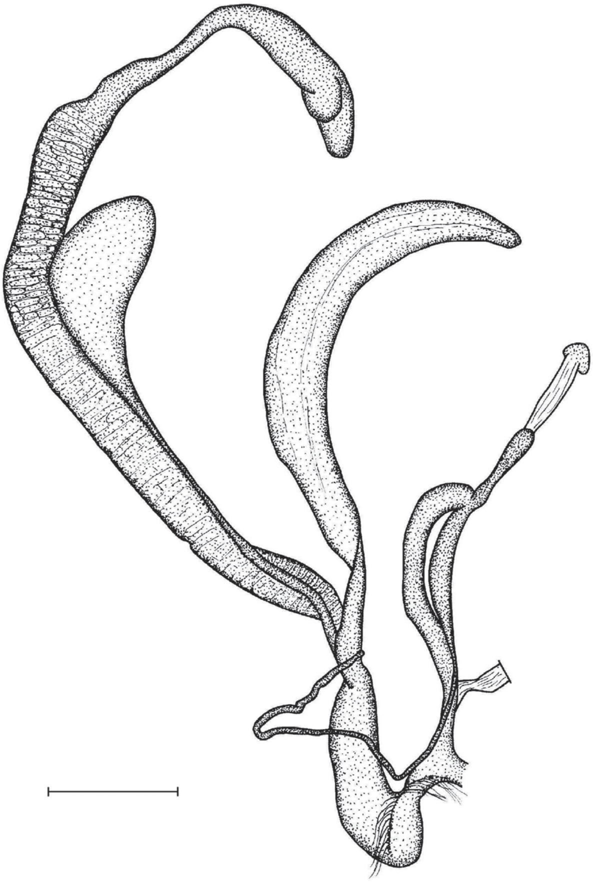

Figure 17. Reproductive anatomy of *Gudeodiscus* (*Gudeodiscus*) *fischeri* (Gude, 1901). Locality information: Tuyên Quang Province, near Ton Hông, road #185 from Tuyên Quang to Vĩnh Lộc (formerly Chiêm Hóa) (NE of Tuyên Quang), leg. Hemmen, Ch. & J., 19.03.2011. Scale represents 5 mm.

IM-2012-2291/24; Tonkin, coll. Balansa 1887, MNHN-IM-2012-2294/4; Halong, MNHN-IM-2012-2295/2; Grotte des Merveilles, coll. Saurin, MNHN-IM-2012-2299/7; Tonkin, coll. Letellier, 1949, MNHN-IM-2012-2304/1; Halong Bay, leg. Messager, MNHN-IM-2012-2316/1; Halong Bay, leg. Messager, MNHN-IM-2012-2317/4; Halong Bay, leg. Messager, MNHN-IM-2012-2322/4; No locality, leg. V. Demange, 29.01.1931, coll. Staadt, 1969, MNHN-IM-2012-2329/298; Tonkin, coll. Denis, MNHN-IM-2012-2332/6; Rochers de Nuy-Dong-Nay, MNHN-IM-2012-2481/529; Tonkin, coll. Staadt. 1969, MNHN-IM-2012-2444/366; Dong-Trien, coll. Blaise, 1902, MNHN-IM-2012-2347/1; Dong-Trien, coll. Blaise, 1903, MNHN-IM-2012-2348/1; Ile de la Table, coll. Staadt, 1969, MNHN-IM-2012-2350/4; Ile Krieu, coll. Blaise, MNHN-IM-2012-2362/2 juvenile shells; Lang-Son, coll. Letellier, 1949, MNHN-IM-2012-2366/1; Ile de la Table, coll. Demange, MNHN-IM-2012-2367/5; Dong-Trieu, coll. Blaise, MN-

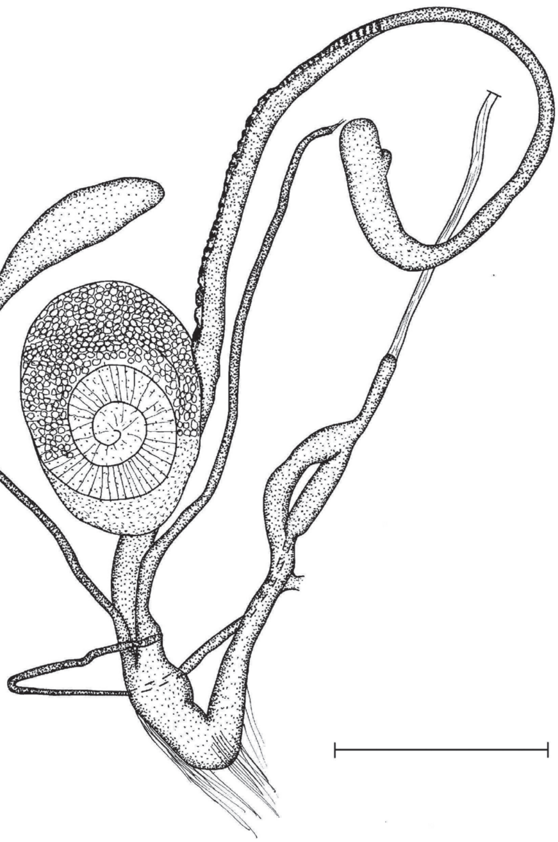

Figure 18. Reproductive anatomy of *Gudeodiscus* (*Gudeodiscus*) *fischeri* (Gude, 1901) (typical *tenuis* specimen). Locality information: Bắc Kạn Province, Ba Bể Nat. Park, Hang Thẳm Kit 2 km from the look-out tower, 335 m, 22°24.686'N, 105°37.710'E, leg. Hunyadi, A., 19.11.2011. Scale represents 5 mm.

HN-IM-2012-2368/2; Halong Bay, leg. Messager, MNHN-IM-2012-2369/3; Halong Bay, leg. Messager, MNHN-IM-2012-2370/3; Halong Bay, leg. Messager, MNHN-IM-2012-2375/6; Tonkin, coll. Fischer, ex Crosse, MNHN-IM-2012-2380/2; Ilots de la Baie d'Along, leg. Messager, MNHN-IM-2012-2381/2; Tonkin, leg. Messager, MNHN-IM-2012-2388/1; Tonkin, coll. Lucas, Acc. no. 2351, NHMUK 20130622/2; Hanoi, Ile de la Table, coll. Biggs, H.E.J. ex Tomlin, 1931, Acc. no. 2258, NHMUK 20130623/8; Tonkin, coll. Salisbury ex Beddome, NHMUK 20130624/1; Tonkin, Ile de la Table, NHMUK 20130625/4; Tonkin, Ile de la Table, NHMUK 1901.12.12.211–212/2; Tonkin, Ile des Merveilles, NHMUK 1901.12.12.232–233/2; Tonquin, NHMUK 1889.9.23.1. (2 shells); Tonkin, Bah-Mun, coll. Dosch ex Rolle, SMF 172085/2 ("*hirsuta*"); Tonkin, Bah-Mun, coll. Ehrmann ex Fruhstorfer, SMF 150137/2 ("*hirsuta*"); Bah-Mun, leg. Fruhstorfer, 29.10.1900, RBINS/2 ("*hirsuta*"); Golfe de Tonkin, coll. Achat Boubée, MNHN-IM-2012-2307/1 ("*hirsuta*"); Tonkin, coll. Salisbury ex Beddome, NHMUK 20110254/1 ("*hirsuta*"); Tonkin, coll. Rolle,

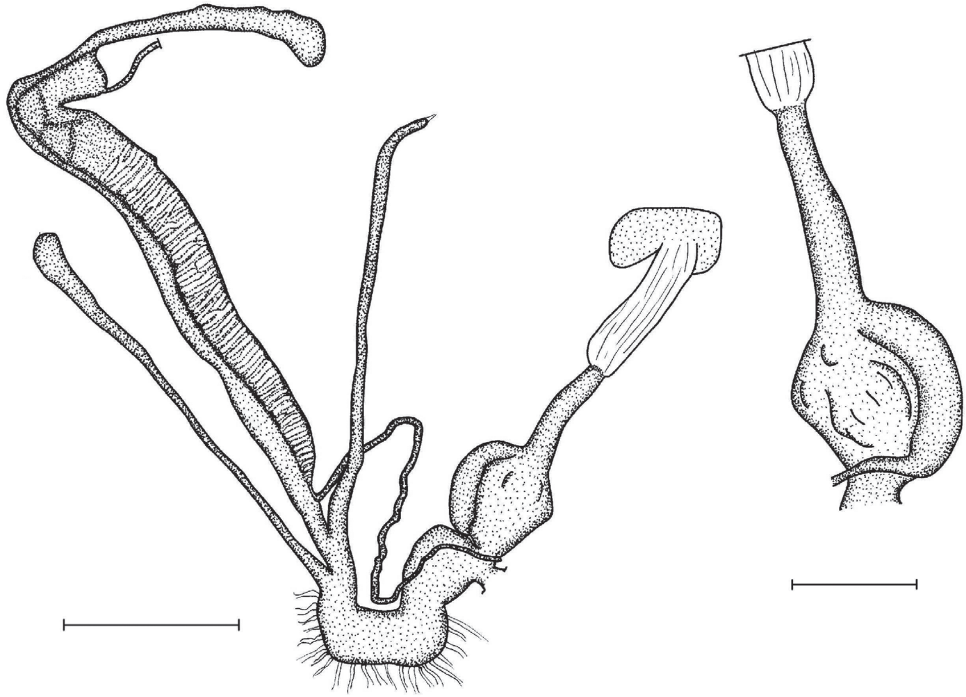

Figure 19. Reproductive anatomy of *Gudeodiscus* (*Gudeodiscus*) *giardi giardi* (Fischer, 1898). Locality information: Cao Bằng Province, Quảng Uyên N, 206–207 cross, 430 m, 22°42.737'N, 106°27.223'E, leg. Hunyadi, A., 16.11.2011. Scales represents 5 mm (left) and 2 mm (right).

4/11/01-25, NHMUK 20110264/3 ("*hirsuta*"); Tonkin, NHMUK 1916.3.16.10/1 ("*hirsuta*"); Tonkin, Bah-Mun, NHMUK 1901.12.23.32–34/3 ("*hirsuta*"); Tonkin, That-Khé, coll. Werner ex Rolle, NHMW 75000/E/7814/2; Tonkin, That-Khé, coll. Klemm, NHMW 79000/K/17484/3; Golf de Tonking, Ile de la Table, coll. Edlauer, NHMW 75000/E/14744/2; Tonkin, Ile Table, coll. Rušnov, NHMW 92583/2; Ile de la Table, Ban Valong (?), coll. Oberwimmer ex Caziot, NHMW 71640/O/9650/2; Tonkin, Ile de la Table, NHMW 92582/2; Tonkin, coll. Fruhstorfer, NHMW 40849/1; Tonkin, That-Ke, coll. Wagner ex Messager, NHMW 103351/2 (mixed sample with *dautzenbergi*); Tonkin, NHMW 46025/1 ("*hirsutus*"); Cha-Ban, Baie d'Along, Tonkin, coll.Steenberg, ZMUC-GAS-1814/2.

New material examined. 20081119A Hải Phòng Province, Hải Phòng City, Cát Bà Isl., Cát Bà Nat. Park, beyond Mây Bầu, ca 160 m, 20°47.763'N, 107°00.758'E, leg. Ohara, K. 19.11.2008., PGB/2, OK/13; **20071122B** same data, leg. Okubo, K., 22.11.2007., PGB/2; **20071122A** Hải Phòng Province, Hải Phòng city, Cát Bà Island, Cát Bà Nat. Park, near pass in front of Mây Bầu, ca 100 m, 20°47.81769'N, 107°00.42256'E, leg. Ohara, K., 22.11.2007., OK/4, PGB/1; **20081118A** Quảng Ninh Province, Hạ Long Bay, Đầu Gỗ Isl., near Đầu Gỗ Cave, ca 15 m, 20°54.696'N, 107°01.069'E, leg. Ohara, K., 18.11.2008., OK/14, PGB/2; **GS25** Quảng Ninh Prov-

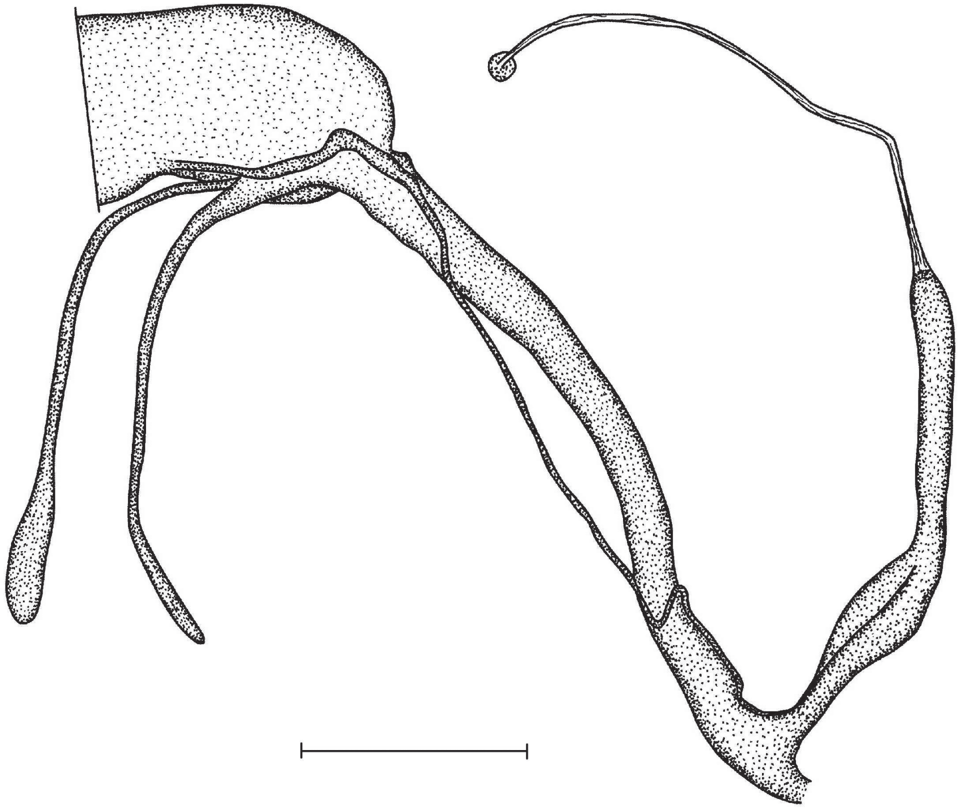

Figure 20. Reproductive anatomy of *Gudeodiscus* (*Gudeodiscus*) *messageri raheemi* Páll-Gergely & Hunyadi, ssp. n. Locality information: Hòa Bình Province, ca. km 156 old road Hà Nội to Sơn La (right side off road), 20°46.000'N, 104°53.885'E, leg. Hemmen, Ch. & J., 15.10.2010. Scale represents 5 mm.

ince, Hạ Long Bay, Đầu Gỗ Cave, N. Đầu Gỗ Island, in leaf litter in limestone crackings, leg. Grego, J., 08.04.2012., PGB/1 broken specimen; **20071122C** Hải Phòng City, Cát Bà Island, Cát Bà N.P., beyond Mây Bầu peak, 165 m, 20°47.70504'N, 107°00.85709'E, leg. Ohara, K., 22.11.2007., PGB/1; **MAA7** Quảng Ninh Province, Hạ Long Bay Area, Áng Dù Island, 20°47.61'N, 107°08.05'E, coll. Maassen, W.J.M., 15.09.2003., PGB/2, WM/8; **MAA8** Hải Phòng Province, Cát Bà Island, half way path lake Ao Ek and Park HQ, 20°47.45'N, 107°00.00'E, leg. Vermeulen, J., coll. Maassen, W.J.M., 27.09.2003. (2 shells); **MAA11** Quảng Ninh Province, Hạ Long Bay Area, Tiên Ông Cave on Hang Trai? Island, collected near the entrance of the cave, 20°48.96'N, 107°07.33'E, coll. Maassen, W.J.M. 06.09.2003., (1 shell).; **no code** Quảng Ninh Province, Hạ Long Bay area, Cây Chanh Island, Cống Đỏ area, 20°52.56'N, 107°11.14'E, leg. Hemmen, Ch. & J., 2003, PGB/2 shells+1jb; **MAA5** same data, coll. Maassen, W.J.M., 13.09.2003., PGB/2, WM/14; **MAA2** Quảng Ninh Province, Hạ Long Bay Area, Cống Đỏ Isl., NE coast, 20°52.44'N, 107°12.10'E, leg. Vermeulen, J., 03.10.2003., coll. Maassen, W.J.M., WM/2; **MAA3** Quảng Ninh Prov-

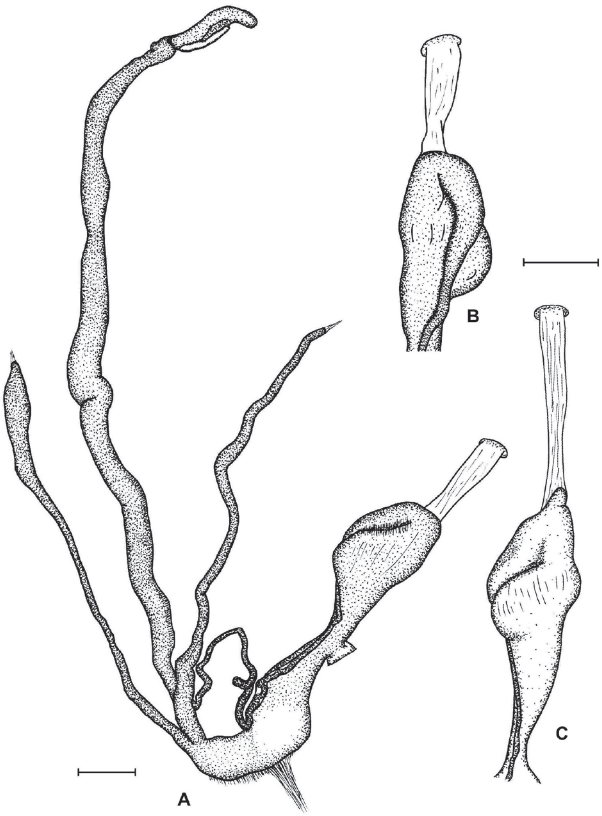

Figure 21. Reproductive anatomy of *Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887) (typical *fallax*). Locality information: Lào Cai Province, ca. 3 km SW of Nhà Văn Hóa, 22°25.513'N, 104°12.194'E, leg. Hemmen, Ch. & J., 04.10.2011. **A–B** "Specimen1" **C** "Specimen2". Scale represents 1 mm.

ince, Hạ Long Bay Area, unnamed island in Cống Đỏ area, 20°52.47'N, 107°11.72'E, coll. Maassen, W.J.M., 03.10.2003., PGB/1, WM/3); **MAA4** Quảng Ninh Province, unnamed island in Đảo Mới Temper area, 20°55.69'N, 107°09.40'E, coll. Maassen, W.J.M., 13.09.2003., PGB/2, WM/18; **MAA6** Quảng Ninh Province, Hạ Long Bay Area, Phao Trong Island, 20°49.80'N, 107°08.32'E, coll. Maassen, W.J.M., 11.09.2003., PGB/1, WM/5; **2012/26** Hải Phòng Province, Đảo Cát Bà (island), Cát Bà Nat. Park, 500 m from the entrance towards Ao Ếch, 60 m, 20°47.945'N, 106°59.653'E, leg. Hunyadi, A., 22.05.2012., HA/1+2jb; **2012/28** Hải Phòng Province, Đảo Cát Bà, Cát Bà Nat. Park, Ao Ếch 500 m towards Mây Bầu, 60 m, leg. Hunyadi, A., 22.05.2012., HA/25+1jb; **2012/32** Quảng Ninh Province, Đèo Bụt (pass) 1 km towards Cẩm Phả, right side of the road, 10 m, 20°58.680'N, 107°11.089'E, leg. Hunyadi, A., 23.05.2012., HA/11+1jb; **2012/34** Quảng Ninh Province, ĐảoTrà Bản (island), Cảng Bản Sen (harbour) 1.5 km towards Cảng Tân Lập (harbour), right side of the road, 30 m, 20°56.943'N, 107°29.772'E, leg. Hunyadi, A., 24.05.2012., HA/84+3jb; **2012/35** Quảng Ninh Province, ĐảoTrà Bản (island), Cảng Bản Sen

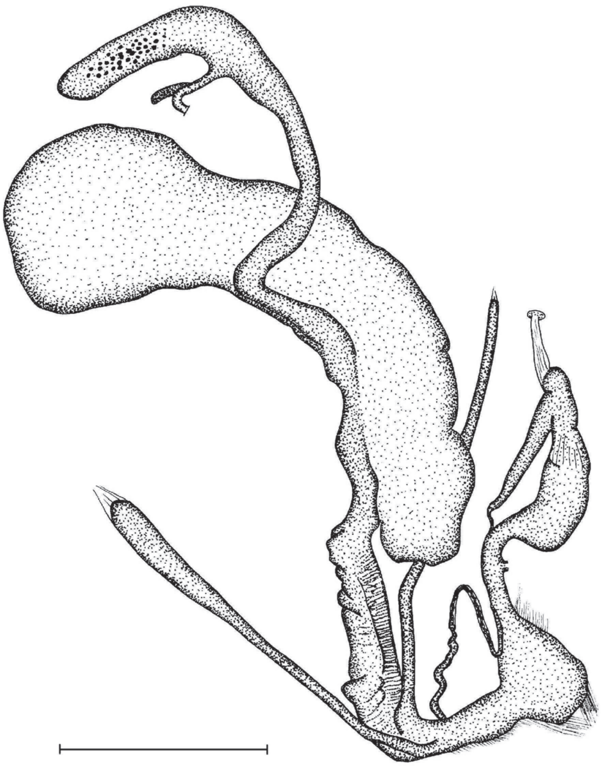

Figure 22. Reproductive anatomy of *Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887). Locality information: Lạng Sơn Province, ca. 10.6 km from Bình Gia to Lạng Sơn on road 1B, 21°53.639'N, 106°25.895'E, leg. Hemmen, Ch. & J., 01.04.2011. Scale represents 5 mm.

(harbour) towards the Cảng Tân Lập (harbour) cross, 200 m, right side of the road, 35 m, 20°56.456'N, 107°29.870'E, leg. Hunyadi, A., 24.05.2012., HA/12; **Vn11-172** Hải Phòng Province, Cát Bà Island, behind cemetery of Gia Luận village, 20°50.092'N, 106°58.560'E, leg. Hemmen, Ch. & J., 10.04.2011., HE/6 (anatomically examined); **Vn11-173** Hải Phòng Province, Cát Bà Island, at km 4 road Gia Luận village to Cát Bà village, 20°49.991'N, 106°58.382'E, leg. Hemmen, Ch. & J., 10.04.2011., HE/11, PGB/1 (in ethanol); **Vn11-174** Hải Phòng Province, Cát Bà Island, between Hiền Hào and Cát Bà village near Xuân Đán, 20°45.479'N, 106°58.556'E, leg. Hemmen, Ch. & J., 10.04.2011., HE/8; **Vn11-175** Hải Phòng Province, Cát Bà Island, between Hiền Hào and entrance of Cát Bà N.P. (road over Hiền Hào), 20°47.681'N, 106°59.068'E, leg. Hemmen, Ch. & J., 11.04.2011., HE/4; **Vn11-38A** Hải Phòng Province, Cát Bà Island, Hoa Cương Cave (=Dong Da Hoang?), near Gia Luận, ca. 30 m, 20°50.268'N, 106°59.019'E, leg. Hemmen, Ch. & J., 10.04.2011., HE/5; **Vn11-165** Quảng Ninh Province, ca. 8.3 km west of Cẩm Phả ca 200 m right of road 18 (no GPS-data), leg. Hemmen, Ch. & J., 03.04.2011., HE/1; **VERM1** Cát Bà, Hải Phòng Province, Cát Bà Island, path from Nat. Park HQ to lake Ao Ek, 20°47.45'N, 107°00.45'E, Pri-

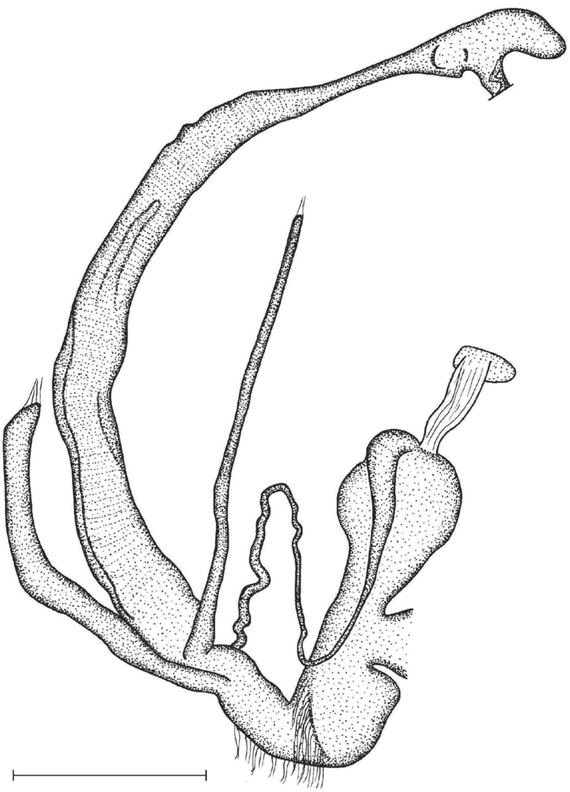

Figure 23. Reproductive anatomy of *Gudeodiscus* (*Gudeodiscus*) *villedaryi* (Ancey, 1888). Locality information: Thái Nguyên Province, Đình Cả NE 4 km, Phượng Hoàng cave, around the entrance of the cave, 365 m, 21°46.782'N, 106°07.189'E, leg. Hunyadi, A., 13.11.2011. Scale represents 5 mm.

mary forest on limestone. Mainly handpicked. leg. Vermeulen, J.J. & Whitten, A.J., 25.09.1998, NHMUK 19991447/4; **VERM3** Hạ Long Quảng Ninh Province, Hạ Long-Cẩm Phả area. Limestone hill S of Hạ Long, with marked regrowth and bamboo thickets, 20°57.00'N, 107°04.43'E, handpicked + soil sample, leg. Vermeulen, J.J. & Whitten, A.J., 28.09.1998 ex Vermeulen, nr. 6527, NHMUK 19991445/3; **20071122D** Hải Phòng Province, Hải Phòng City, Cát Bà Island, Cát Bà Nat. Park, between Cát Bà N.P., ranger st. and Quan Y, GPS not recorded, leg. Ohara, K, Okubo, K. & Otani, J. U., 22.11.2007., coll PGB (in ethanol, anatomically examined).

Diagnosis. Shell medium-sized to very large, thick shelled, almost smooth or with very fine periostracal ribs; apertural lip well-developed; apertural fold long, more or less equally long in its total length, connected to the callus. Parietal wall with missing or short anterior lamella (always distant from the upper plica) and well-developed posterior lamella; palatal plicae depressed Z-shaped.

Measurements (in mm). D = 16.6–17.1, H = 8.3–8.5 (n=2, MAA5); D = 17.4–19.9, H = 7.9–9.2 (n=2, MAA4); D = 16.1–19.8, H = 7–9.4 (n=2, MAA6); D = 23.1–23.4, H = 10.8–11 (n=2, 20081119A); D = 24.8–25.6, H = 11.7–13 (n=4, Vn11-

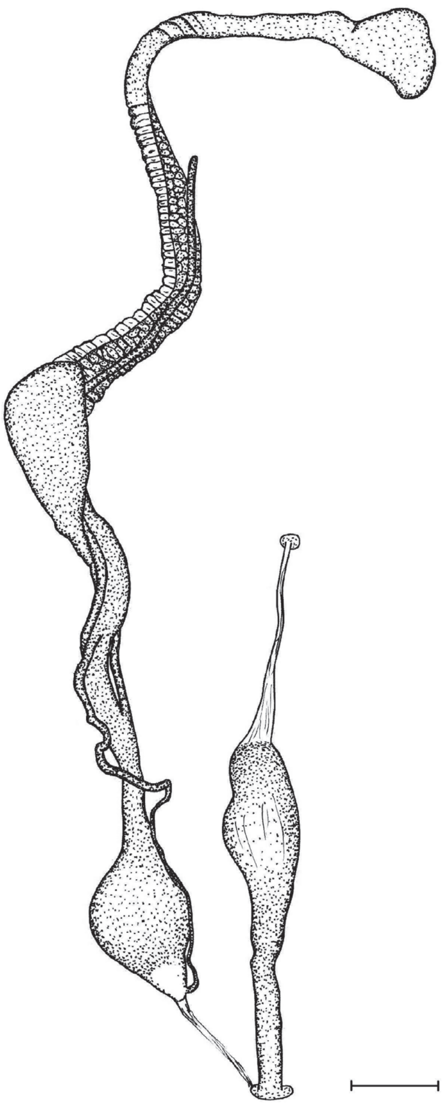

Figure 24. Reproductive anatomy of *Gudeodiscus* (*Gudeodiscus*) *villedaryi* (Ancey, 1888), abnormal specimen. Locality information: Thái Nguyên Province, Võ Nhai District, Phú Thượng Commune, Phượng Hoàng Cave, Mỏ Gà Vill., ca 150 m, 21°46.836'N, 106°07.107'E, leg. Ohara, K., 20.05.2009. Scale represents 2 mm.

174); D = 26–28.1, H = 12.8–13.1 (n=3, Vn11-175); D = 16.9–17.4, H = 8.2–8.4 (n=3, NHMUK 20110264, "*hirsuta*"); D = 16.5–17.3, H = 8.1–8.5 (n=3, NHMUK 1901.12.23.32–34, "*hirsuta*") (see also Figure 44).

Differential diagnosis. *Gudeodiscus dautzenbergi* and some populations of *G. villedaryi* resemble *Halongella schlumbergeri* in terms of general, but the inner lamellae are entirely different, namely, *G. dautzenbergi* and *G. villedaryi* have strong, well-developed anterior lamella with an anteriorly elongated lower "leg", whereas most *H. schlumbergeri*

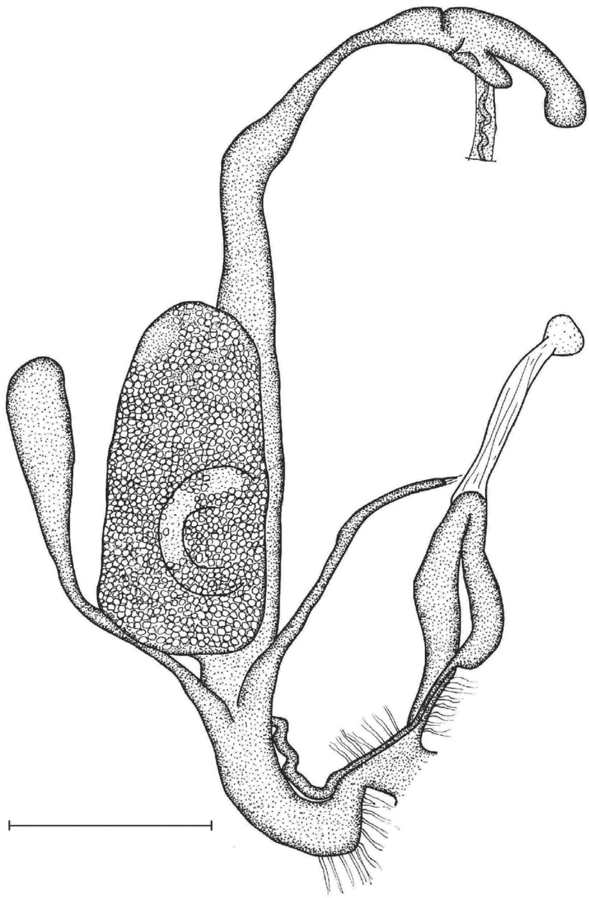

Figure 25. Reproductive anatomy of *Halongella fruhstorferi* (Möllendorff, 1901). Locality information: Quảng Ninh Province, Vân Đồn Island (NE Cẩm Phả), Cái Rồng village, 21°3.560'N, 107°25.551'E, leg. Hemmen, Ch. & J., 14.08.2011. Scale represents 5 mm.

shells lack the anterior lamella. It is possible to distinguish *H. schlumbergeri* from the other two species without breaking the shell, on the basis of the long apertural fold reaching the callus, which is short in *G. dautzenbergi* and *G. villedaryi*, and has an elevated "knob" part in some distance from the callus. See also under *H. fruhstorferi*.

Intraspecific diversity. The species is very variable in terms of shell size and the formation of plicae and lamellae on the parietal wall.

Description of the genitalia. Two specimens were examined anatomically each from one of two different samples. "Specimen1": Hải Phòng Province, Cát Bà Island, behind cemetery of Gia Luận village, 20°50.092'N, 106°58.560'E, leg. Hemmen, Ch. & J., 10.04.2011. (with embryo in its uterus, Figures 26, 29H, 33B, F); "Specimen2": Hải Phòng Province, Hải Phòng City, Cát Bà Island, Cát Bà Nat. Park, between Cát Bà N.P., ranger st. and Quan Y, GPS not recorded, leg. Ohara, K, Okubo, K. & Otani, J. U., 22.11.2007. (without embryo in its uterus, Figures 29A–B, 30G–I, 33A, C–E, G).

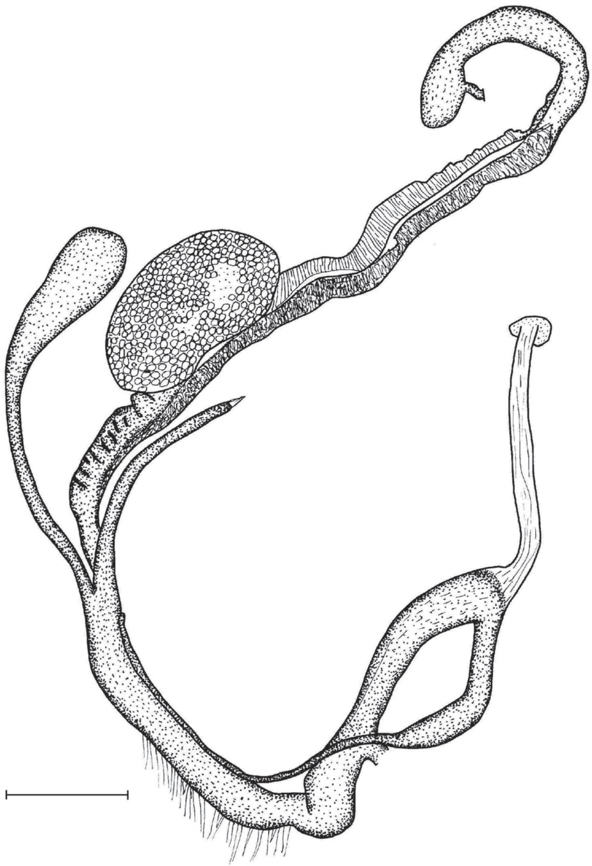

Figure 26. Reproductive anatomy of *Halongella schlumbergeri* (Morlet, 1886), "Specimen1". Locality information: Hải Phòng Province, Cát Bà Island, behind cemetery of Gia Luận village, 20°50.092'N, 106°58.560'E, leg. Hemmen, Ch. & J., 10.04.2011. Scale represents 5 mm.

Penis relatively long, slimmer proximally and slightly thicker distally; inner wall with several (16–18) parallel running folds (Figures 29A–B); between the folds flat, T-shaped calcareous granules were found (both specimens had granules between the folds, see Figures 30G–I); epiphallus of similar length to the penis, proximally thicker than distally; its inner wall with six parallel folds; on the distal portion of the epiphallus the longitudinal folds have several perpendicular projections which overlap with those of the neighbouring fold (Figures 29H); penial caecum absent, the retractor muscle inserts on the penis-epiphallus transition. Vagina long, with a weak vaginal bulb; it is attached to the body wall with several filaments of connective tissue; inner wall of the vagina with 6–11 parallel, rather regular longitudinal folds; in "Specimen2" there are several, translucent calcareous granules on the folds; the granules have a widened base portion which attaches to the folds, and an apical part with some (1–10) pointed needles (Figure 33A, C–E, G); "Specimen1" had tiny rounded granules ("sand") in the vagina lumen, not attached to the vagina wall (Figure 33F); stalk of the gametolytic

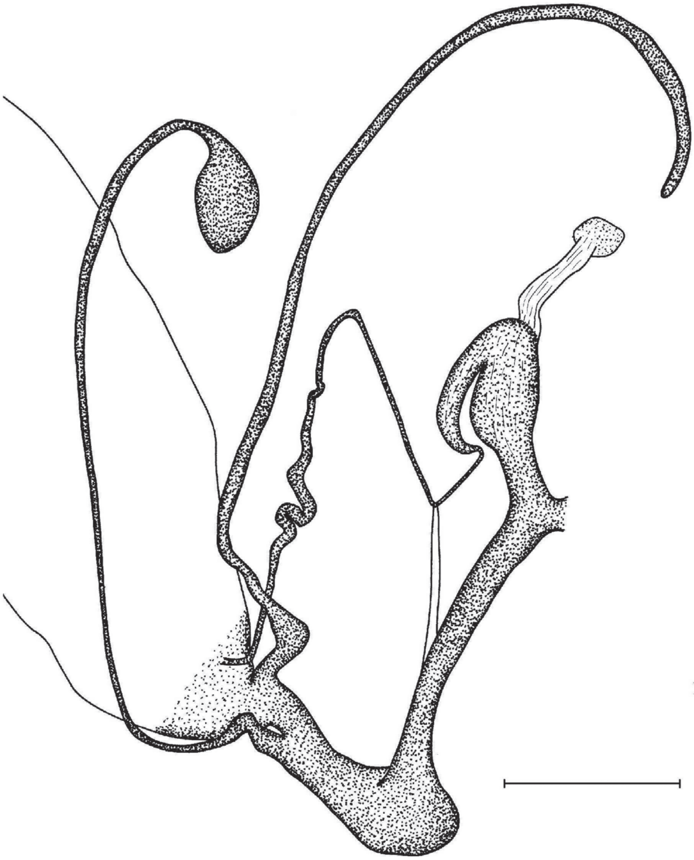

Figure 27. Reproductive anatomy of *Sicradiscus mansuyi* (Gude, 1908). Locality information: Cao Bằng Province, southern edge of Pác Rải, Trùng Khánh 3 km towards Quảng Uyên, left side of the road, 570 m, 22°48.961'N, 106°30.533'E, leg. Hunyadi, A., 28.05.2012. Scale represents 2 mm.

sac with conspicuously thickened gametolytic sac is longer than the much slimmer diverticulum.

Radula. See Table 6 and Figures 36D–F.

Distribution (see Figures 40 and 44). The species has only been recorded in the Hạ Long Bay area (Hải Phòng and Quảng Ninh provinces).

Remarks. Gude (1901b) figured specimens of all three "species": *schlumbergeri*, *jovia* and *villedaryi* (later re-named *pilsbryana*). His observations were based on one specimen from each "species". He wrote the following: "A comparison of these three species has shown that that they are very closely allied, and that there is no difference of diagnostic value between the armature. They differ, however, in external aspect sufficiently to rank as separate forms. *P. jovia* is the largest of the three, while *P. villedaryi* is the smallest, *P. schlumbergeri* being intermediate in size." The additional differences mentioned by Gude, namely the strength of the callus, direction and small differences in the shape of the palatal and parietal lamellae and plicae are not sufficient to separate species. We had the possibility to observe and measure a number of shells collected in the Hạ Long Bay Area and provided with exact GPS data. The outer shell characters exhibit little variation other than in size. Therefore, we suggest synonymising the three species under one name.

The shell differences between *Plectopylis schlumbergeri* (and its synonyms) and *Plectopylis hirsuta*, namely the short or missing anterior lamella in *schlumbergeri* and the relatively "normal" anterior lamella of *hirsuta* are considered to be very minor. This trait shows clinal variation across shells assigned to *hirsuta* and *schlumbergeri* (and its synonyms). We therefore synonymize *Plectopylis hirsuta* with *Halongella schlumbergeri*.

Genus *Sicradiscus* Páll-Gergely, 2013

Type species. *Plectopylis schistoptychia* Möllendorff, 1886, by original designation.

Diagnosis. See introduction.

Differential diagnosis. *Gudeodiscus* differs from the keeled shell of *Sicradiscus* by the rounded body whorl. *Sicradiscus* species having rounded body whorl differ from *Gudeodiscus* by the combination of small shells with glossy base, a strong apertural fold connected to the callus, and short or divided palatal plicae. In contrast, *Gudeodiscus* species have usually large, mainly finely ribbed shells with weak apertural folds free from the callus (often absent) and long, depressed Z-shaped palatal plicae. See also under *Halongella* gen. n. and under the Discussion.

Sicradiscus mansuyi (Gude, 1908)

Figures 2A, 9H, 11A–B, 27, 31A, 36J–L

1908 *Plectopylis Mansuyi* Gude, Journal de Conchyliologie, 55: 347, 348–351., Figs 2a–e, Plate 7., Figs 1–3. ["Ha-Lang, Tonkin"]

2013 *Sicradiscus mansuyi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde, 142 (1): 50.

Types examined. Tonkin, Ha-Lang, leg. Mansuy, NHMUK 1907.2.20.19 (syntype, Figure 2A).

Museum material examined. Ha-Lang, coll. Mansuy, MNHN-IM-2012-2365/6; Ha-Lang, leg. Mansuy, MNHN-IM-2012-2384/7; HaLang, Tonkin, coll. Steenberg, ZMUC-GAS-1808/2.

New material examined. **20081116C** Cao Bằng Province, Trùng Khánh District, Cảnh Tiên Commune, Pắc Rảo Village, ca 545 m, 22°48.941'N, 106°30.549'E, leg. Ohara, K., 16.11.2008., OK/66, PGB/5; **2011/81** Cao Bằng Province, Đèo Mã Phục (pass) 500 m towards Quảng Uyên, left side of the road, rock cavern, 610 m, 22°43.981'N, 106°20.333'E, leg. Hunyadi, A., 14.11.2011., HA/10; **2012/43** Cao Bằng Province, Pắc Rảo, Cảnh Tiên Commune cross, 300 m towards Trùng

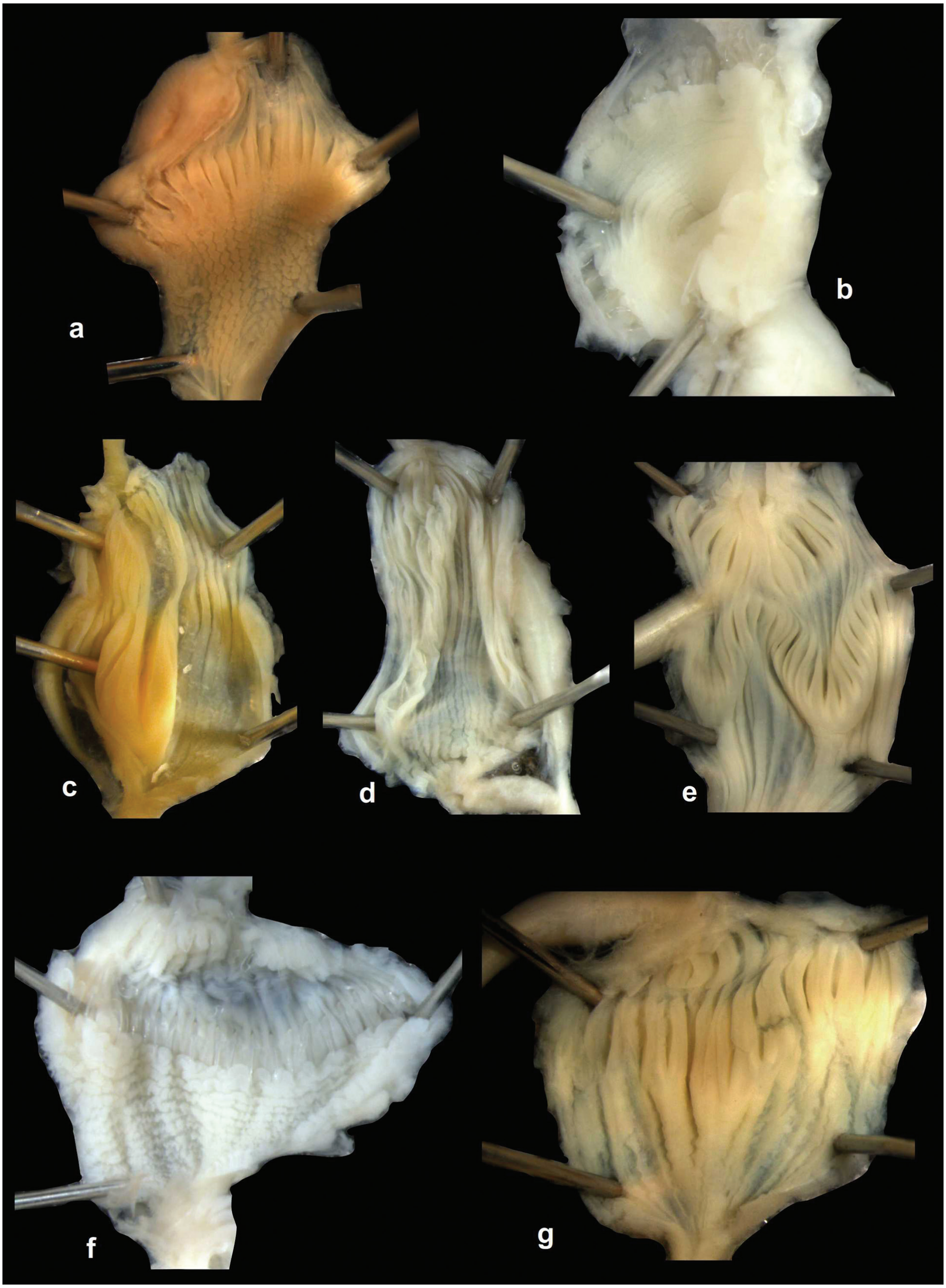

Figure 28. Inner walls of the penis of *Gudeodiscus* Páll-Gergely, 2013, species. **A** *Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887) (typical *fallax* specimen, for locality see Figure 21) **B** *Gudeodiscus giardi giardi* (Fischer, 1898) (for locality see Figure 19) **C** *G.* (*G.*) *phlyarius* (Mabille, 1887) (for locality see Figure 22) **D** *G.* (*G.*) *fischeri* (Gude, 1901) (for locality see Figure 17) **E** *G.* (*G.*) *messageri raheemi* Páll-Gergely & Hunyadi, ssp. n., 20080510A **F–G** *G.* (*G.*) *villedaryi* specimens collected at the same locality in two different dates: **F** November (2011/102) and **G** May (20090520A). All photos by B. Páll-Gergely.

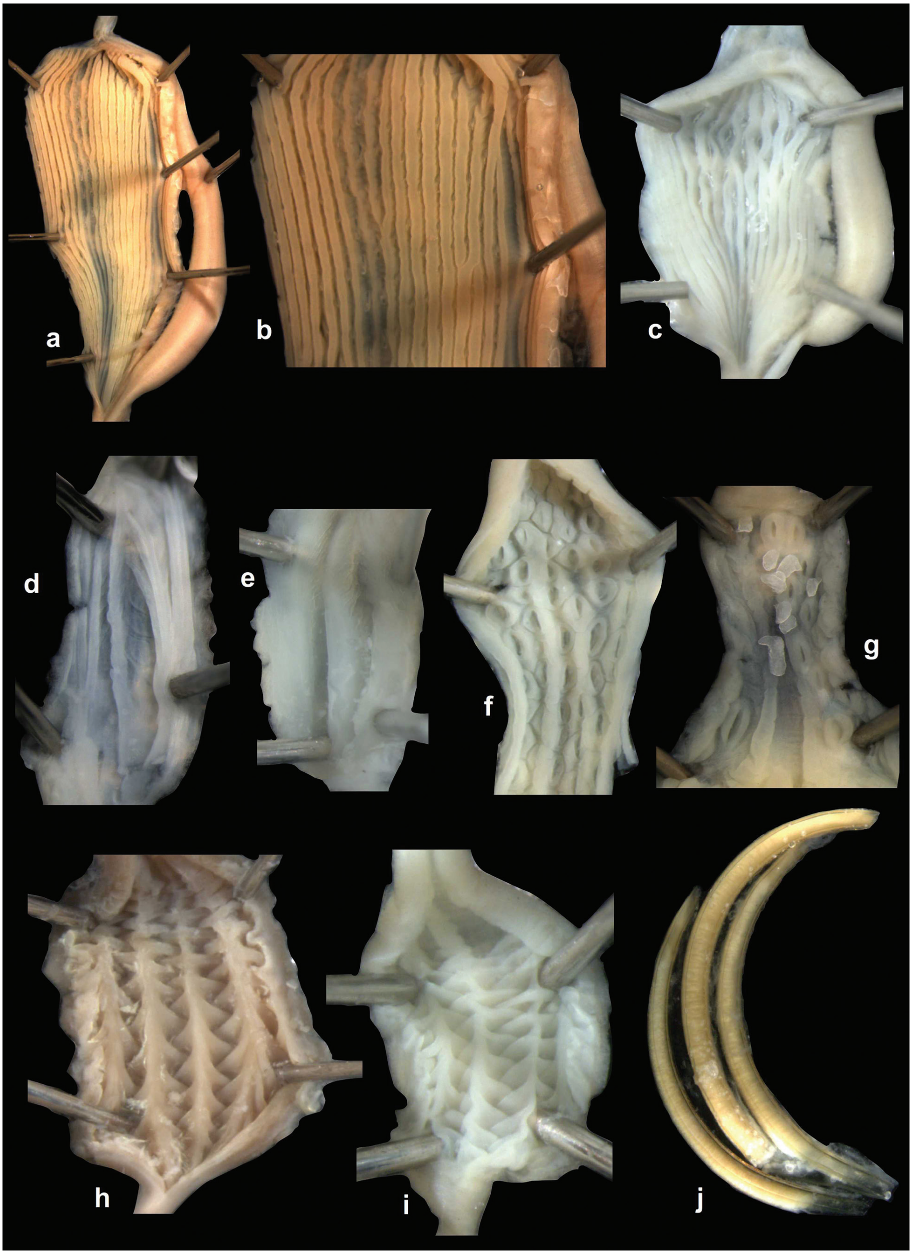

Figure 29. Inner walls of male reproductive organs of *Gudeodiscus* and *Halongella* gen. n. species. **A–B** penis of *Halongella schlumbergeri* (Morlet, 1886), 20071122D **C** penis of *Halongella fruhstorferi* (Möllendorff, 1901) (for locality see Figure 25) **D** epiphallus of *Gudeodiscus fischeri* (Gude, 1901), (for locality see Figure 18) **E** epiphallus of *Gudeodiscus giardi giardi* (Fischer, 1898), (for locality see Figure 19) **F** penial caecum of *G.* (*G.*) *messageri raheemi* Páll-Gergely & Hunyadi, ssp. n. (for locality see Figure 20) **G** penial caecum of *G.* (*G.*) *messageri raheemi* ssp. n. (for locality see Figure 28E) **H** epiphallus of *H. schlumbergeri* (for locality see Figure 26) **I** *H. fruhstorferi*, (for locality see Figure 25) **J** spermatophore of *G.* (*G.*) *fischeri*, (for locality see Figure 17). All photos by B. Páll-Gergely.

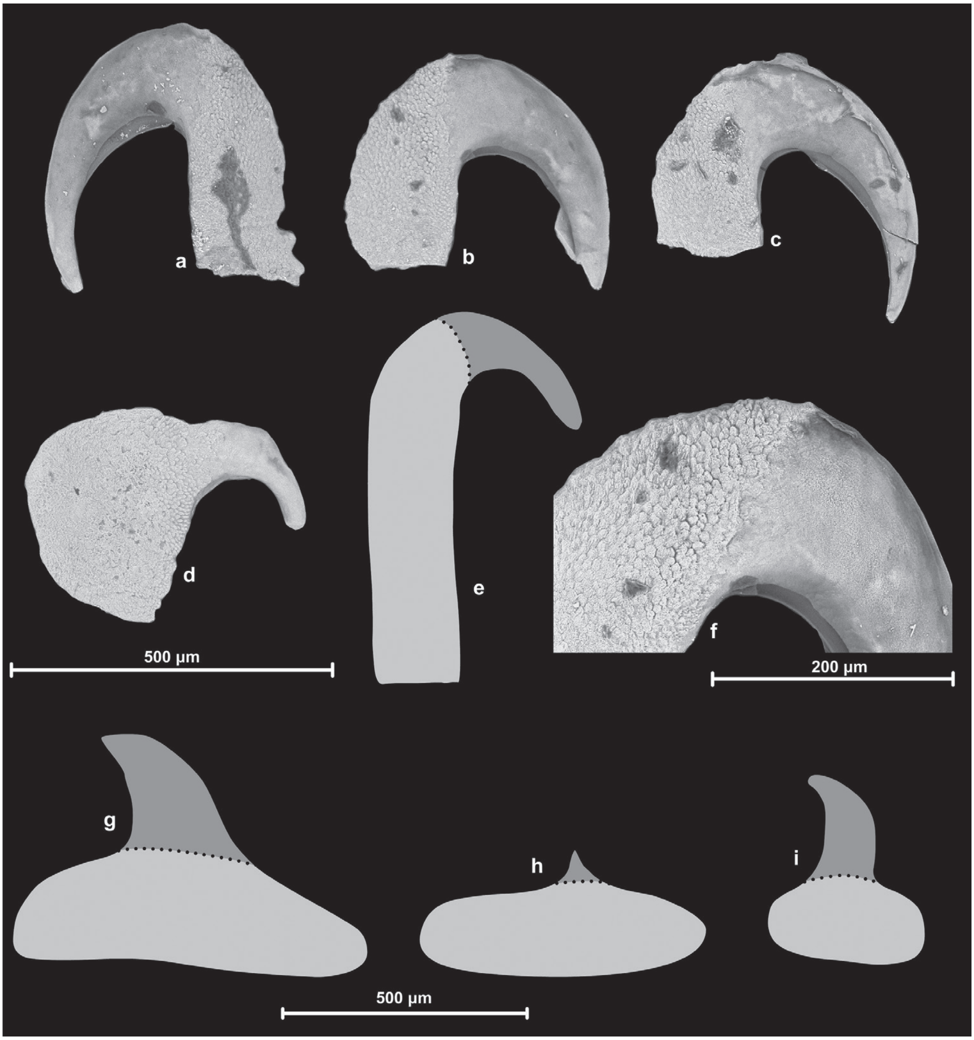

Figure 30. Calcareous claws found in pockets on the inner penial wall of *Gudeodiscus* and *Halongella* gen. n. species. **A–C, F** *Gudeodiscus* (*Gudeodiscus*) *villedaryi* (Ancey, 1888) (for locality see Figure 23) **D** *Gudeodiscus giardi giardi* (Fischer, 1898) (for locality see Figure 19) **E** *G.* (*G.*) *fischeri* (Gude, 1901) (for locality see Figure 19) **G–I** *Halongella schlumbergeri* (Morlet, 1886) (for locality see Figure 29A–B). The claws in case of *G.* (*G.*) *fischeri* and *H. schlumbergeri* were too fragile for dissecting out, therefore drawings are presented. All images by B. Páll-Gergely.

Khánh, right side of the road, 530 m, 22°49.385'N, 106°30.742'E, leg. Hunyadi, A., 28.05.2012., HA/9+5 jb; **2012/44** Cao Bằng Province, southern edge of Pắc Rảo, Trùng Khánh 3 km towards Quảng Uyên, left side of the road, 570 m, 22°48.961'N, 106°30.533'E, leg. Hunyadi, A., 28.05.2012., HA/226; **2012/47** Hà Giang Province, Hà Giang 105.5 km towards Đồng Văn, Vân Chải Commune, left side of the road 4C, 23°09.084'N, 105°10.774'E, leg. Hunyadi, A., 31.05.2012., HA/4; **Vn11-141** Hà

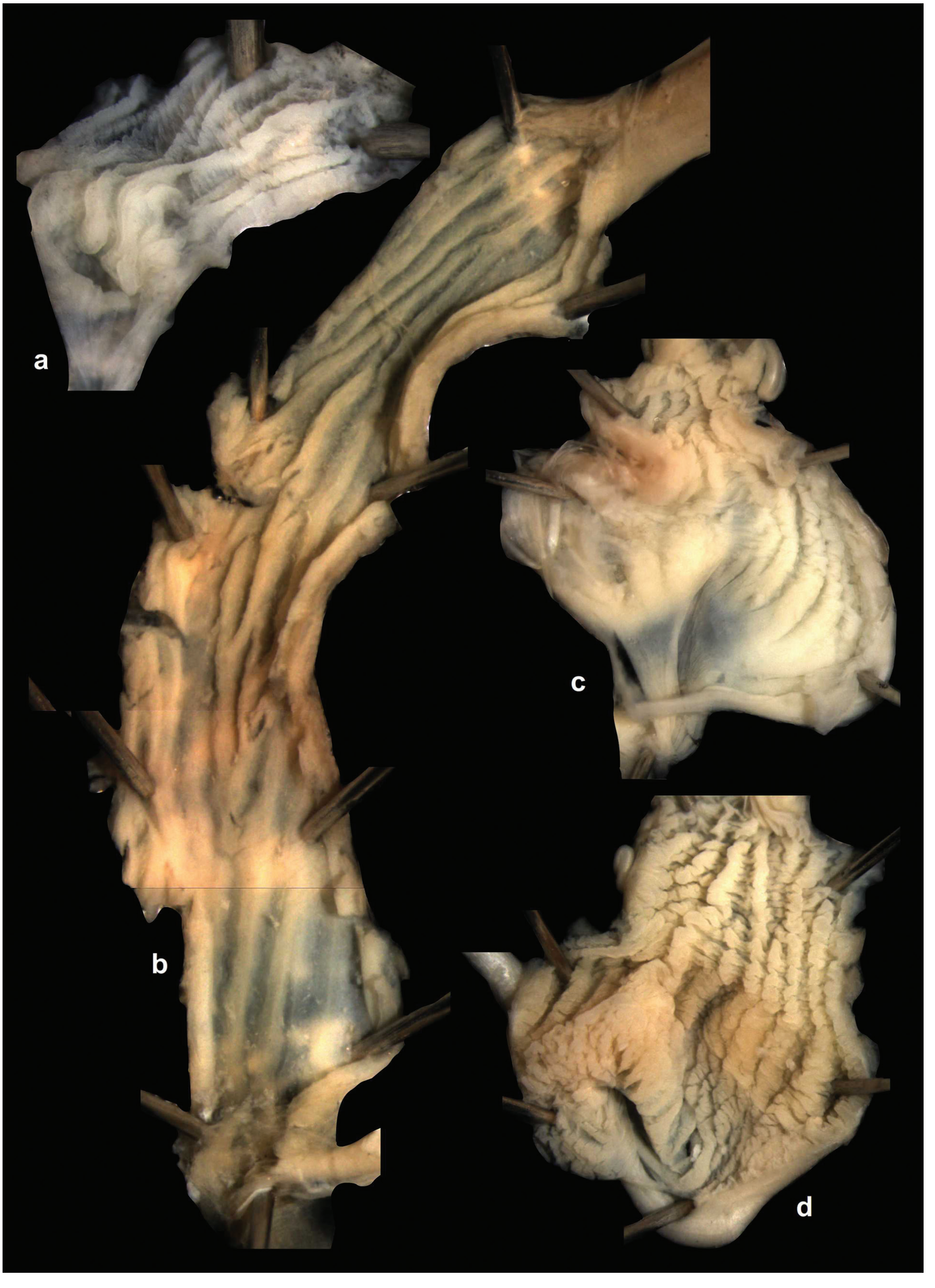

Figure 31. Inner wall of the vagina of *Sicradiscus* and *Gudeodiscus* species. **A** *Sicradiscus mansuyi* (Gude, 1908), (for locality see Figure 27) **B** *Gudeodiscus* (*Gudeodiscus*) *messageri raheemi* Páll-Gergely & Hunyadi, ssp. n. (for locality see Figure 20) **C** *Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887), Vn11-157 **D** *Gudeodiscus* (*Gudeodiscus*) *fischeri* (Gude, 1901) (for locality see Figure 17).

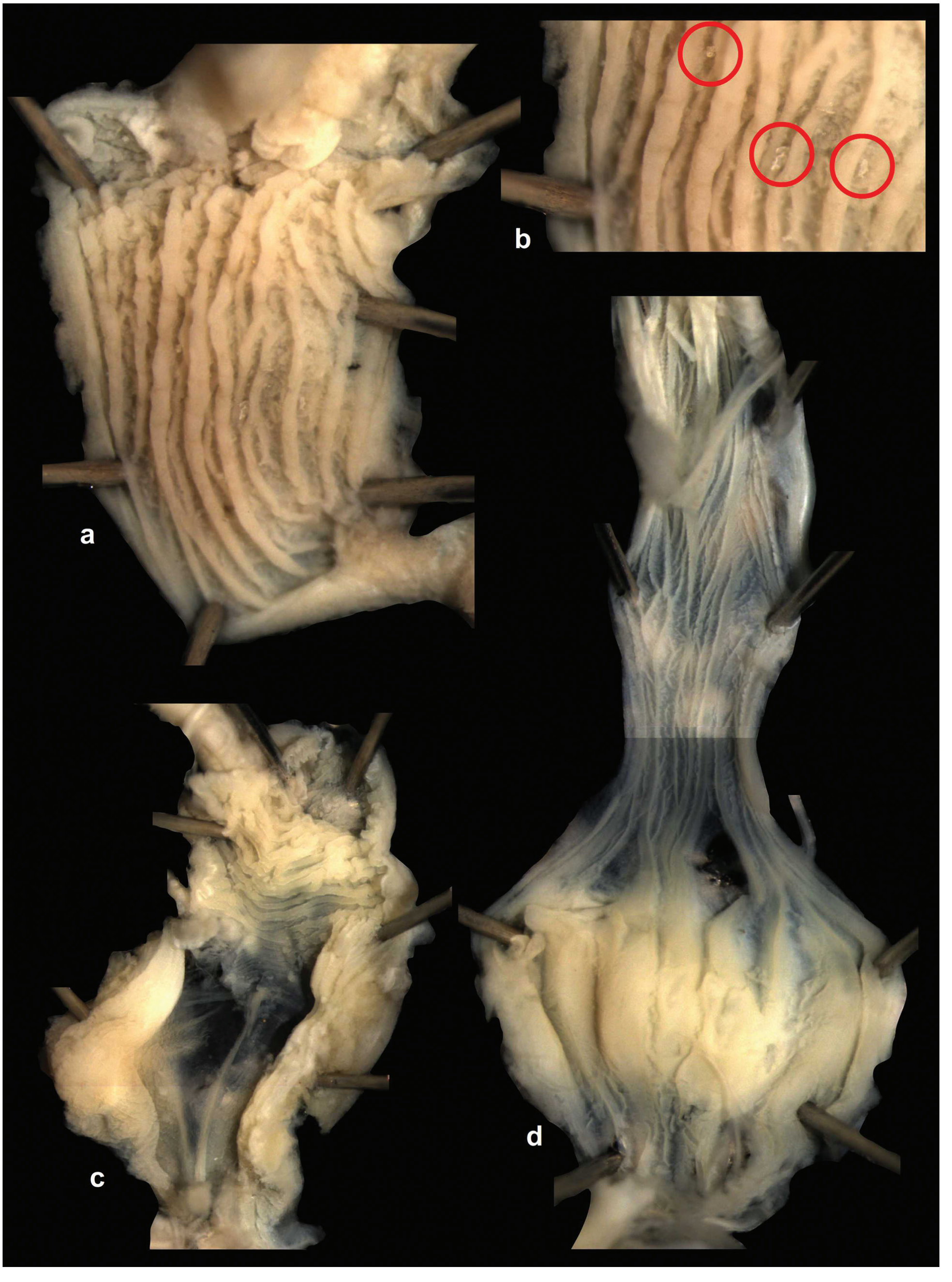

Figure 32. Inner wall of the vagina of *Halongella* gen. n. and *Gudeodiscus* species. **A–B** *Halongella fruhstorferi* (Möllendorff, 1901), red circles indicate calcareous granules (for locality see Figure 25) **C** *Gudeodiscus* (*G.*) *giardi giardi* (Fischer, 1898) (for locality see Figure 19) **D** *G.* (*G.*) *villedaryi* (Ancey, 1888) (for locality see Figure 24).

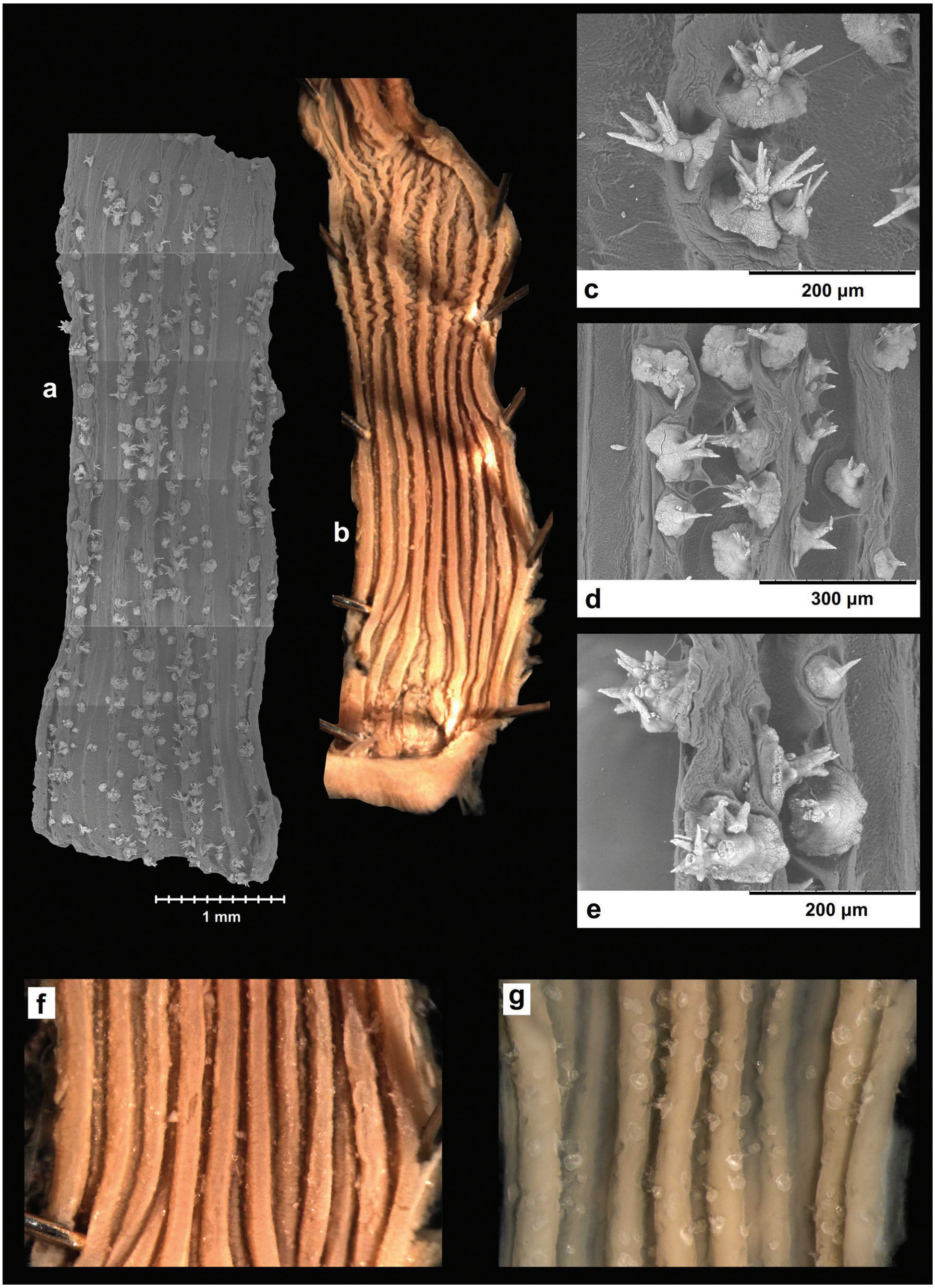

Figure 33. Inner wall of the vagina (**A–B, F–G**) and vaginal granules (**C–E**) of *Halongella schlumbergeri* (Morlet, 1886). "Specimen1" (gravid specimen, locality Vn11-172): **B, F**; "Specimen2" (not gravid specimen, locality 20071122D): **A, C–E, G**.

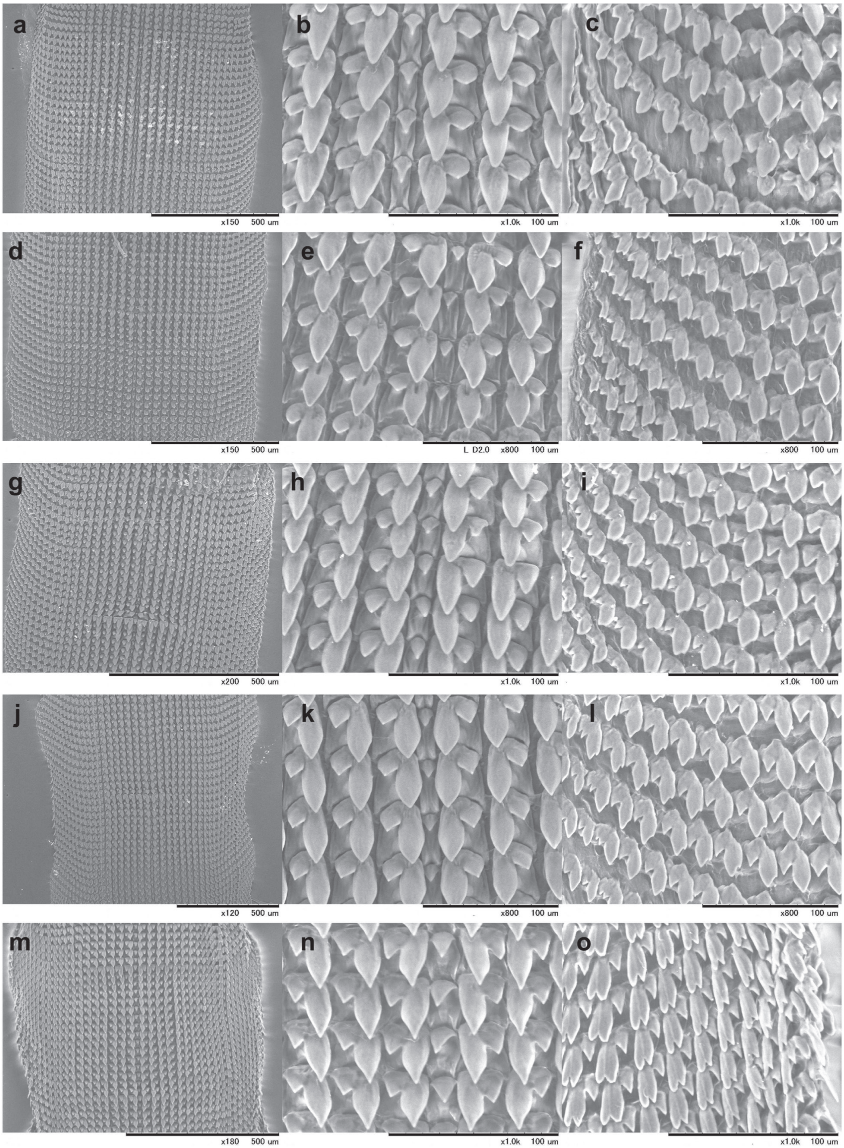

Figure 34. SEM images of radulae of *Gudeodiscus* species. **A, D, G, J, M** show the middle part of the radula **B, E, H, K, N** show the central tooth and the first 2–3 pairs of laterals **C, F, I, L, O** show the marginals. **A–C** *Gudeodiscus* (*Veludiscus*) *emigrans otanii* Páll-Gergely & Hunyadi, 2013, China, Guangxi, Yizhou Shi, Aishan Xiang, Xiannuyan, ca 170 m, 24°29.292'N, 108°34.057'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 13.11.2004. **D–F** *G.* (*V.*) *eroessi eroessi* Páll-Gergely & Hunyadi, 2013, China, Guangxi, Guigang Shi, Guzhang Xiang, beyond Chuanshan village, ca 155 m, 23°20.848'N, 109°19.256'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 09.11.2004 **G–I** *G.* (*V.*) *okuboi* Páll-Gergely & Hunyadi, 2013, Guangxi, Guigang Shi, Guzhang Xiang, road to Wushan Xiang, ca 130 m, 23°21.178'N, 109°17.432'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 09.11.2004. **J–L** *G.* (*V.*) *pulvinaris pulvinaris* (Gould, 1859), China, Hong Kong Peak, leg. Miu Yeung, June 2013 **M–O** *G.* (*G.*) *fischeri* (Gude, 1901), (for locality see Figure 17). All photos by B. Páll-Gergely.

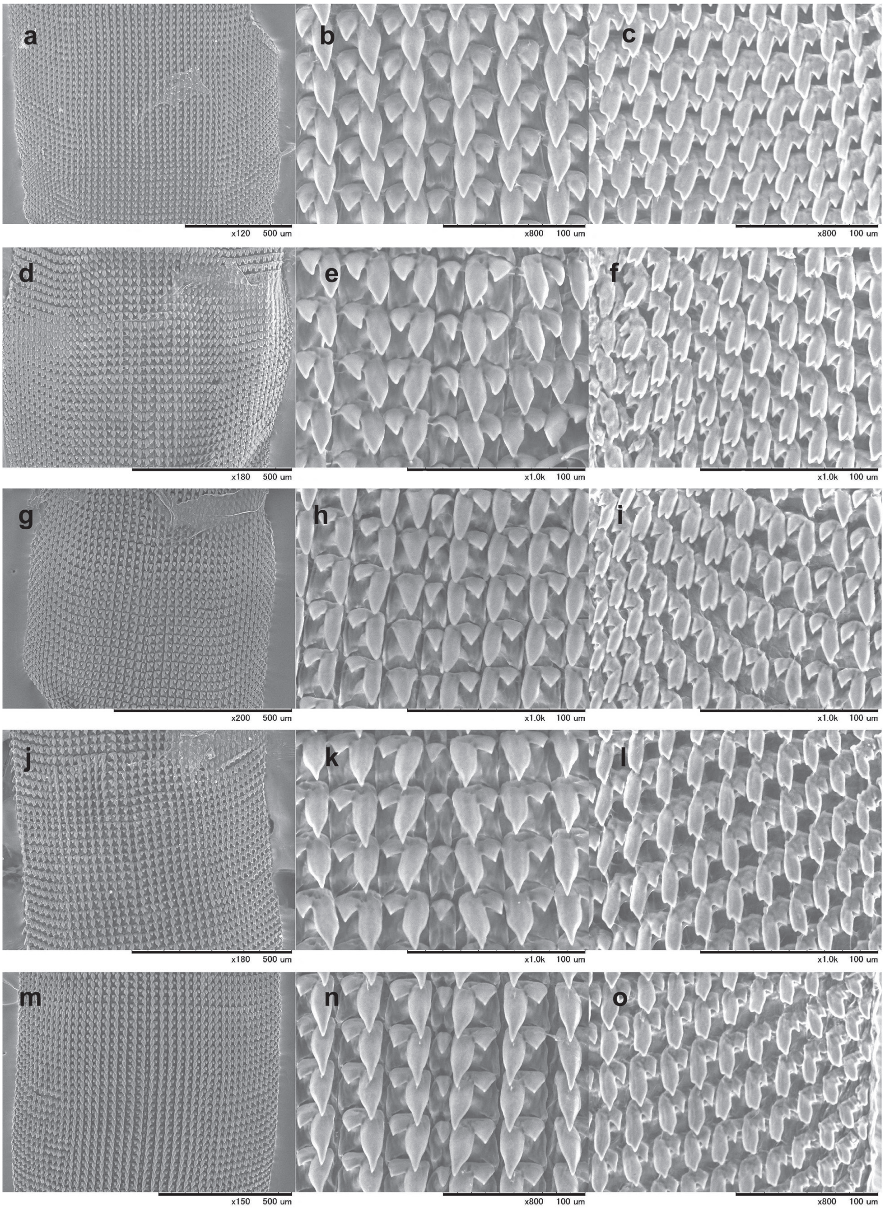

Figure 35. SEM images of radulae of *Gudeodiscus* species. **A, D, G, J, M** show the middle part of the radula **B, E, H, K, N** show the central tooth and the first 2–3 pairs of laterals **C, F, I, L, O** show the marginals. **A–C** *Gudeodiscus* (*Gudeodiscus*) *giardi giardi* (Fischer, 1898) (for locality see Figure 19) **D–F** *G.* (*G.*) *messageri raheemi* Páll-Gergely & Hunyadi, ssp. n. (for locality see Figure 20) **G–I** *G.* (*G.*) *multispira* (Möllendorff, 1883), China, Guangxi, Qingshan, Qingshan Zhen, Lipu Xian, ca 250 m, 24°26.189'N, E110°20.008'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 12.11.2004. **J–L** *G.* (*G.*) *phlyarius* (Mabille, 1887), Lạng Sơn Province, ca. km. 50 of road 1B, 10 km to Bình Gia, 21°53.911'N, 106°25.664'E, leg. Hemmen, Ch. & J., 01.04.2011. **M–O** *G.* (*G.*) *villedaryi* (Ancey, 1888), (for locality see Figure 23). All photos by B. Páll-Gergely.

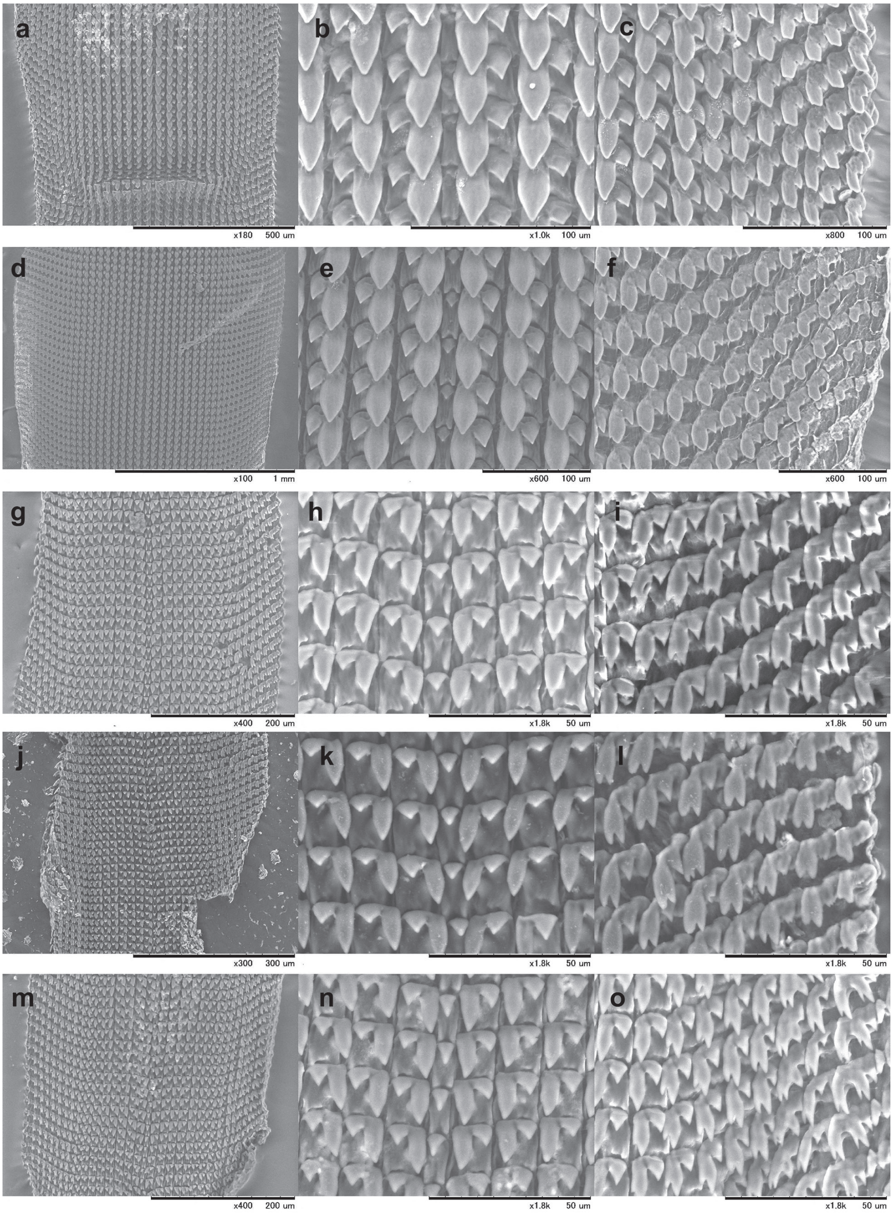

Figure 36. SEM images of radulae of *Halongella* and *Sicradiscus* species. **A, D, G, J, M** show the middle part of the radula; **B, E, H, K, N** show the central tooth and the first 2–3 pairs of laterals **C, F, I, L, O** show the marginals. **A–C** *Halongella fruhstorferi* (Möllendorff, 1901) (for locality see Figure 25) **D–F** *H. schlumbergeri* (Morlet, 1886) (for locality see Figure 29A–B) **G–I** *Sicradiscus invius* (Heude, 1885), China, Sichuan, Dujiangyan Shi, Taian Zhen, Sanlong Shuijingrongdong, ca 1090 m, 30°55.039'N, 103°29.662'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 17.09.2013. **J–L** *S. mansuyi* (Gude, 1908), (for locality see Figure 27) **M–O** *S. schistoptychia* (Möllendorff, 1886), China, Hunan, Yongzhou Shi, Ningyuan Xian, Jiuyishan Yaozuxiang, Jiuyishan Guojia Senlin Gongyuan, old maple forest, 25°21.200'N 111°58.696'E, 450 m, leg. Hunyadi, A., 11.11.2010. All photos by B. Páll-Gergely.

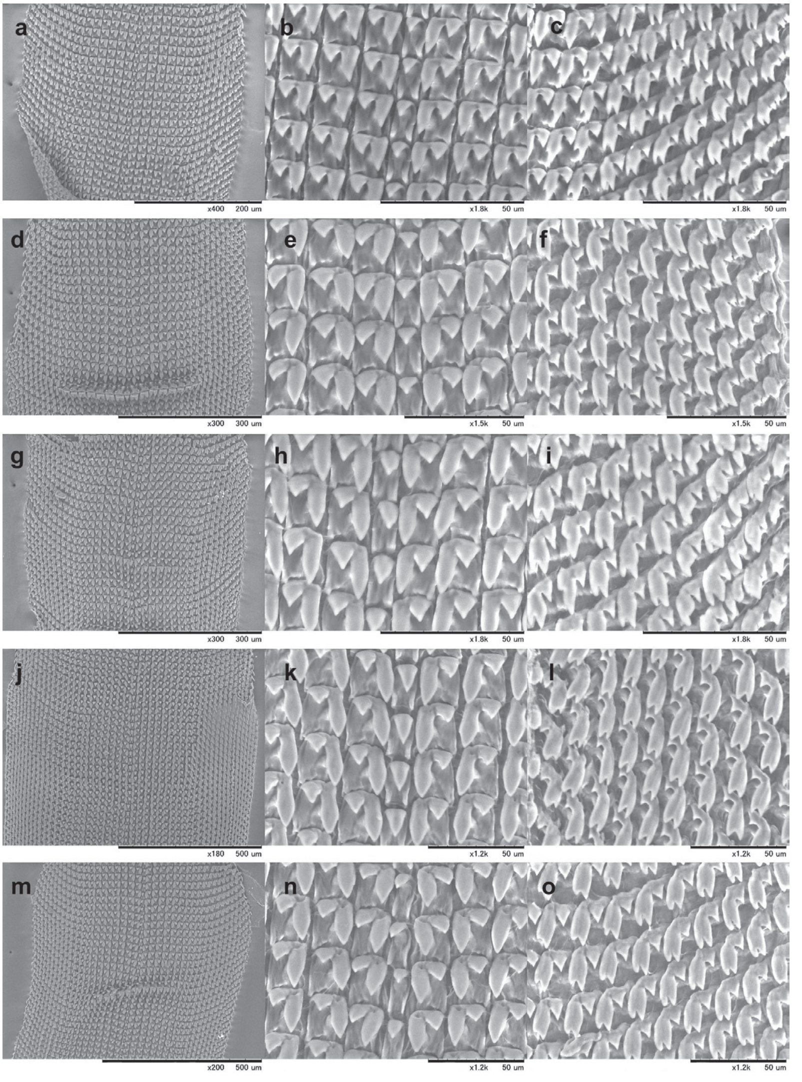

Figure 37. SEM images of radulae of *Sicradiscus* and *Sinicola* species. **A, D, G, J, M** show the middle part of the radula **B, E, H, K, N** show the central tooth and the first 2–3 pairs of laterals **C, F, I, L, O** show the marginals. **A–C** *Sicradiscus transitus* Páll-Gergely, 2013, Guangxi, Hechi Shi, Tiane Xian, Qimu Xiang, near Lahaoyan, 650 m, 24°51.359'N, 107°11.407'E, leg. Hunyadi, A. & Szekeres, M., 12.09.2013. **D–F** *Sinicola asamiana* Páll-Gergely, 2013, Sichuan, Dujiangyan Shi, Qingchengshan Zhen, Jinbian Yan, 30°55.234'N, 103°29.483'E, 930 m, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 16.09.2013. **G–I** *S. emoriens* (Gredler, 1881), Hunan, Yongzhou Shi, Lingling Qu, Dengjiachong, rocky wall, 125 m, 26°13.808'N, 111°35.907'E, leg. Hunyadi, A., 8.11.2010. **J–L** *S. fimbriosa* (von Martens, 1875), China, Hunan, Hengyang Shi, Nanyue Qu, Yuelin Xiang, southern part of Heng Shan, Chuanyan Shilin, near Ban Shanting, 590 m, 27°16.435'N 112°42.195'E, leg. A. Hunyadi 20.10.2010. **M–O** *S. jugatoria* (Ancey, 1885), China, Hubei, Yichang Shi, Changyang Tujiazu Zizhixian, Qingjiang Hualang Fengjingqu, Geheyan Shuiku, Wuluozhougli Shan, 260 m, 30°25.805'N 110°59.254'E, leg. A. Hunyadi 31.10.2010. All photos by B. Páll-Gergely.

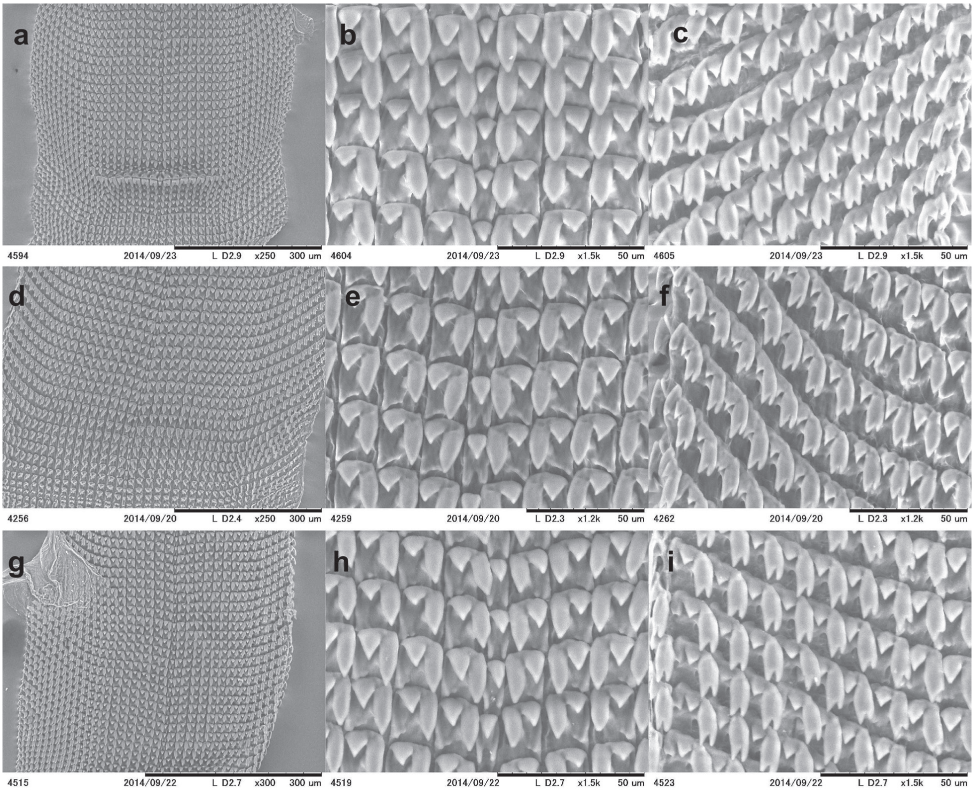

Figure 38. SEM images of radulae of *Sinicola* species. **A, D, G** show the middle part of the radula **B, E, H** show the central tooth and the first 2–3 pairs of laterals **C, F, I** show the marginals. **A–C** *Sinicola murata* (Heude, 1885), Sichuan, Dujiangyan Shi, Qingchengshan Zhen, Jinbian Yan, 30°55.234'N, 103°29.483'E, 930 m, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 16.09.2013. **D–F** *S. reserata azona* (Gredler, 1887), Guizhou, Tongren Shi, Wanshanchen dirt road, Xianrendong, ca 865 m, 27°31.785'N, 109°13.008'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.5.2010. **G–I** *S. stenochila* (Möllendorff, 1885), Hubei, Enshi Tujiazu Miaozu Zizhizhou, Badong Xian, Badong E, Bashan Senlin Gongyuan, 300 m W from the entrance, 220 m, 31°01.684'N, 110°25.094'E, leg. Hunyadi, A., 3.11.2010. All photos by B. Páll-Gergely.

Giang Province, km 105.5 on road 4c, between Yên Minh and Đồng Văn (NE of Hà Giang town), 23°08.996'N, 105°10.332'E, leg. Hemmen, Ch., 21.03.2011., HE/6; **Vn11-143** Hà Giang Province, km 120 on road 4c, between Yên Minh and Đồng Văn (NE of Hà Giang town), no GPS-data, leg. Hemmen, Ch. & J., 22.03.2011., HE/3; **Vn10-60** Cao Bằng Province, ca. 6.5 km from Quảng Uyênto Mã Phục (left off road), 22°41.293'N, 106°23.422'E, leg. Hemmen, Ch. & J., 24.03.2010., HE/2; **20050327A** China, Guangxi (广西), Daxin Xian (大新), Xialei Zhen (下雷鎮), Detianpubu (德天瀑布) (Detian waterfalls), leg. Ohara, K. & Moriya Shigeki, 27.03.2005., PGB/1 (with glossy dorsal surface and without denticles posterior to the palatal plicae).

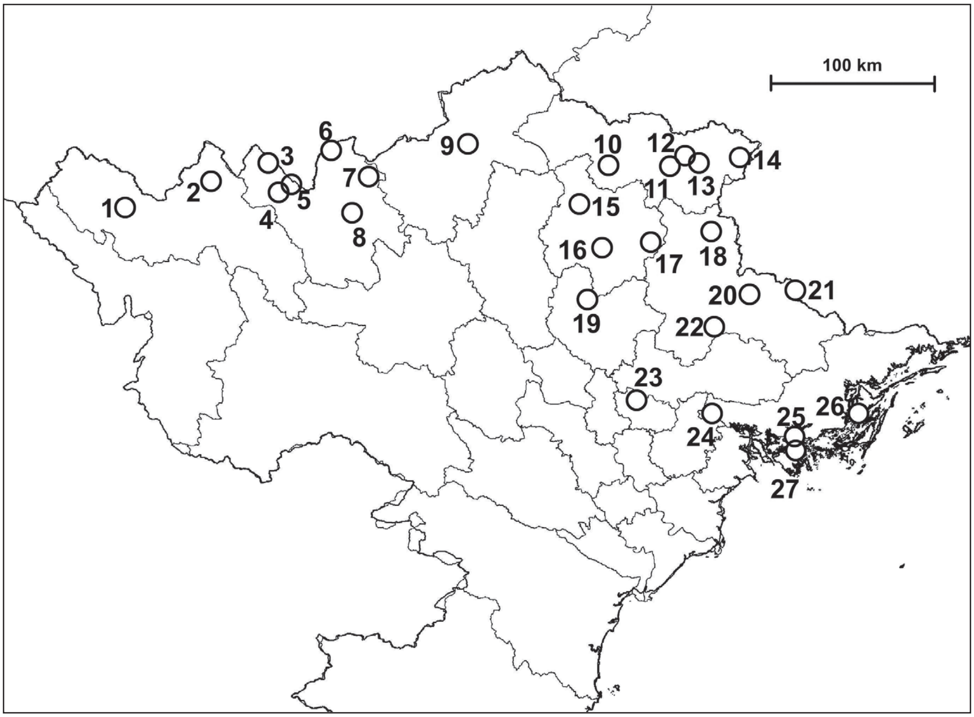

Figure 39. Locations mentioned in literature on plectopylid taxonomy. **1** Muong-Bo **2** Phony-Tho **3** Trinh-Thuong **4** Muong-Hum **5** Nat-Son (Nhat Son) **6** Muong-Kong **7** Long-Ping **8** Pac-Kha **9** Ha-Giang **10** Tinh-Tuc **11** Cao-Bang **12** Déo-Ma-Phuc **13** Quang-Huyen **14** Ha-Lang **15** Cho-Ra **16** Bac-Khan **17** Nac-Ri **18** That-Khé **19** Cho-Moi **20** Lang-Son **21** Mansongebirge **22** Than-Moi **23** Bac-Ninh **24** Dong-Trieu **25** Bah-Mun **26** Kebao **27** Baie d'Along. The locations of "Col de Nuages" (Clouds Pass) could not be located. It is probably situated on Lao Kay Province, close to Muong-Hum.

Diagnosis. A very small species with reticulated dorsal and glossy ventral surface, elevated spire, elevated, sharp callus and well-developed apertural fold connected to the callus (Figure 9H). Parietal wall with two lamellae, the anterior one separated from both the lower and upper plicae; middle palatal plicae short, connected with a ridge and sometimes ornamented with small denticles posteriorly (Figures 11A–B).

Measurements (in mm). D = 6.7–7, H = 3.4–3.9 (n=4, 20081116C).

Differential diagnosis. All other similar congeners inhabit China. *Sicradiscus feheri* Páll-Gergely & Hunyadi, 2013 is larger, flatter with a wider umbilicus and a shinier dorsal surface, has a longer, horizontal palatal plicae without additional posterior denticles, and has a more elevated and longer apertural fold. *Sicradiscus transitus* Páll-Gergely & Hunyadi, 2013 has a lower spire and a wider umbilicus with slightly shouldered whorls, sometimes strong radial lines on the ventral surface, and a more elevated callus. Moreover, the anterior lamella of *S. transitus* is in contact with both the upper and the lower plicae, which are free from the lamella in *S. mansuyi*. *Sicradiscus invius* is flatter (has shallower umbilicus) with only the protoconch

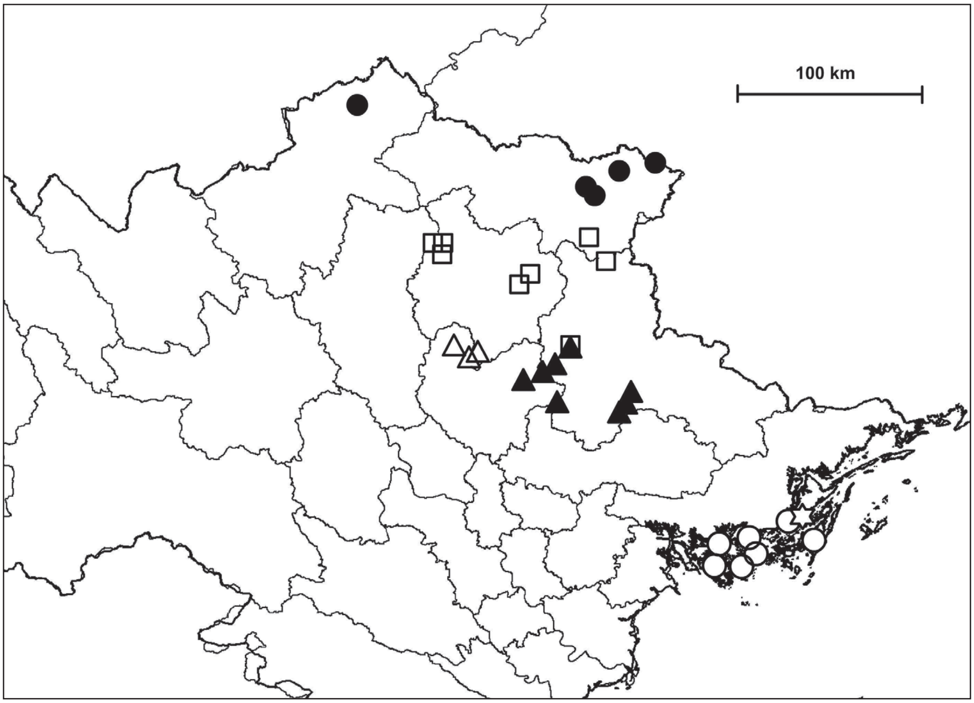

Figure 40. Distribution of *Gudeodiscus*, *Halongella* gen. n. and *Sicradiscus* species. Legends: empty circle: *Halongella schlumbergeri* (Morlet, 1886), star (close to the circles): *H. fruhstorferi* (Möllendorff, 1901), empty triangle: *Gudeodiscus* (*Gudeodiscus*) *dautzenbergi* (Gude, 1901), filled triangle *G.* (*G.*) *villedaryi* (Ancey, 1888), empty square: *G.* (*G.*) *anceyi* (Gude, 1901), filled circle: *Sicradiscus mansuyi* (Gude, 1908).

elevated from the dorsal surface; it has weaker dorsal sculpture resulting in a glossy surface (*mansuyi* is densely reticulated), and lacks the additional small denticles posterior to the palatal plicae, which are usually present in *S. mansuyi*. *Gudeodiscus anceyi* is larger and has a ribbed shell with spiral lines on the whole shell. Species possessing a glossy ventral surface (*G. cyrtochilus*, *G. fischeri*) are also larger and have weaker or no apertural fold.

Intraspecific diversity. Low; shell characters stable. The species is easily recognisable and can be separated from other plectopylid species without difficulty.

Description of the genitalia. Two specimens were anatomically examined (Cao Bằng Province, southern edge of Pắc Rảo, Trùng Khánh 3 km towards Quảng Uyên, left side of the road, 570 m, 22°48.961'N, 106°30.533'E, leg. Hunyadi, A., 28.05.2012. (Figures 27, 31A).

Penis with a shorter, slimmer proximal section and a thinner, somewhat longer distal portion; internally with parallel folds which are more elevated in the thinner distal portion, forming pocket-like structures (similar to that of *S. transitus*, see Páll-Gergely and Asami 2014); these "pockets" did not contain granules; epiphallus approximately as long as the penis but much slimmer; internally penis and epiphallus wall with longi-

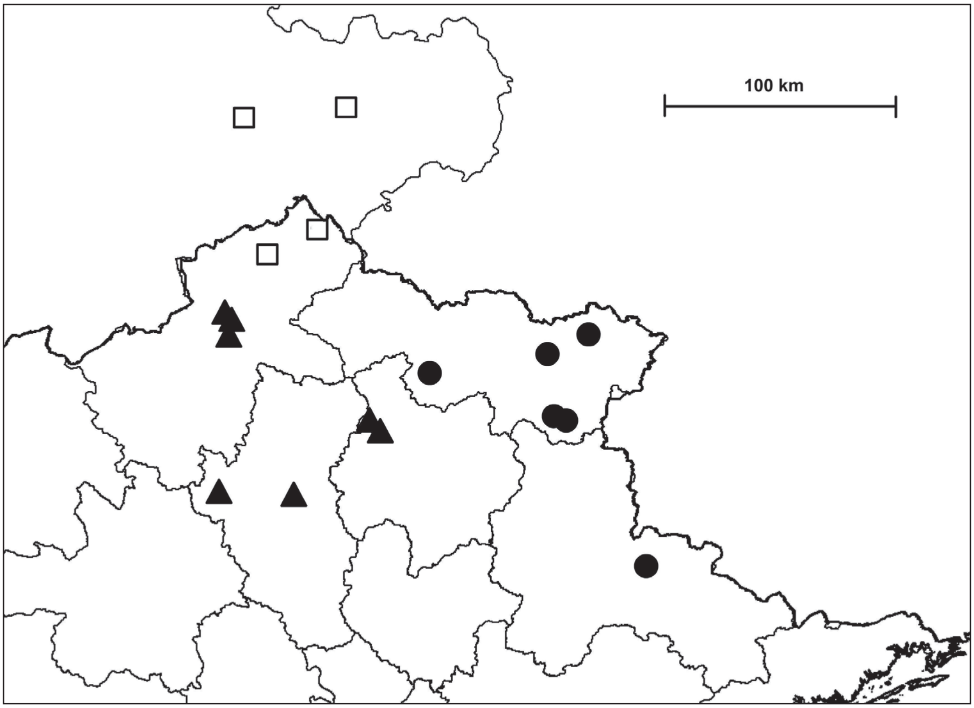

Figure 41. Distribution of *Gudeodiscus* species. Legends: filled circle: *Gudeodiscus* (*Gudeodiscus*?) *suprafilaris* (Gude, 1908), triangle: *G.* (*G.*) *fischeri* (Gude, 1901), empty square: *G.* (*G.*?) *cyrtochilus* (Gude, 1909).

tudinal, parallel folds; retractor muscle short, inserts on the penis-epiphallus transition; penial caecum absent. Vagina long, with distal vaginal bulb; vaginal bulb and other parts of the vagina with approximately 8, more or less parallel, serrulate folds (Figure 31A); vas deferens long, thicker distally and more slender proximally; gametolytic sac and diverticulum are of equal length, in parallel.

Radula. See Table 6 and Figures 36J–L.

Distribution. This species was described from Hạ Lang (eastern part of Cao Bằng Province, see Figure 39). We have seen newly collected material from northern Hà Giang and Cao Bằng provinces. The first occurrence of the species from China is reported. This locality is situated very close to the Vietnamese border.

Concluding remarks

Identification and species recognition

For this revision of the Vietnamese Plectopylidae, we examined the type specimens of all known taxa, 197 newly collected specimens with detailed locality data and 631 historical lots deposited in a variety of public collections. Altogether we examined

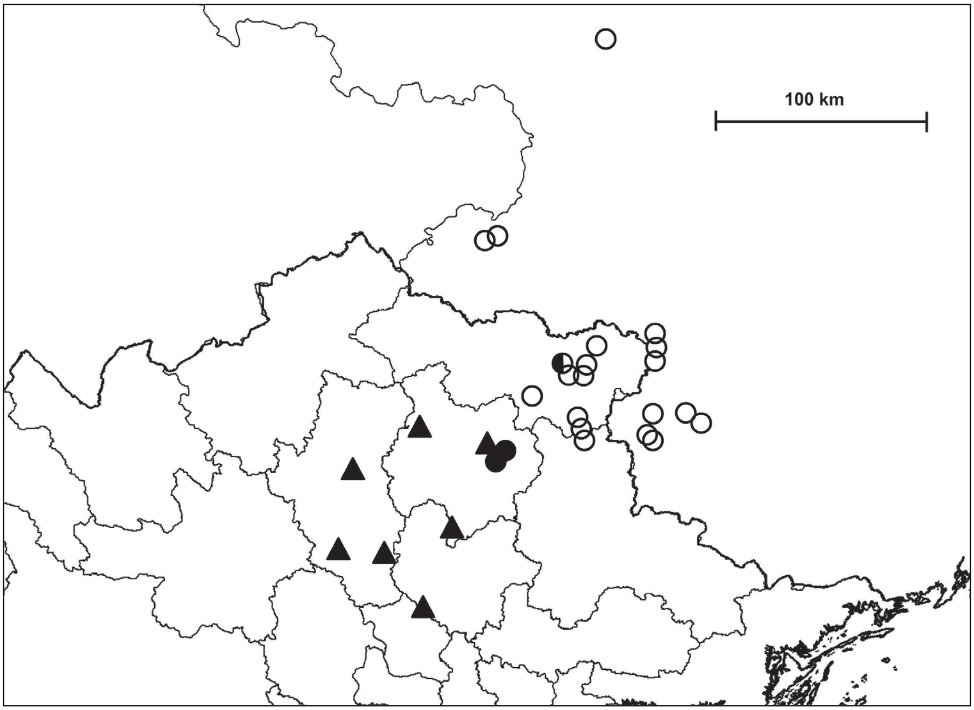

Figure 42. Distribution of *Gudeodiscus* species. Legends: filled triangle: *Gudeodiscus* (*Veludiscus*) *emigrans quadrilamellatus* Páll-Gergely, 2013, empty circle: *G.* (*G.*) *giardi giardi* (Fischer, 1898), filled circle: *G.* (*G.*?) *francoisi* (Fischer, 1899), semi filled circle: co-occurrence of the latter two species.

more than 7000 shells (see Table 12). We found specimens of most species in European museum collections, probably because of intensive shell exchanges at the beginning of the 20th Century. The present scale of specimen examination allowed us to understand species boundaries in the Vietnamese Plectopylidae better than the preceding studies.

Although the plicae and lamellae (especially on the parietal wall) are common characteristics of the family and useful for identification of some species, their value in species recognition has been somewhat overestimated. This appears to have led to descriptions of several species that differ only slightly in palatal and parietal plication. Our recognition of distinct species is primarily based on general shell and aperture shape, and secondarily on the morphology of plicae and lamellae.

Key characters for identification (see also identification key)

As a summary, below we present the most important shell characters for identification of each species from others within the Vietnamese Plectopylidae. In the case of *Gudeodiscus emigrans emigrans* and *G. infralevis*, however, available shell specimens were insufficient to provide help for "routine" identification.

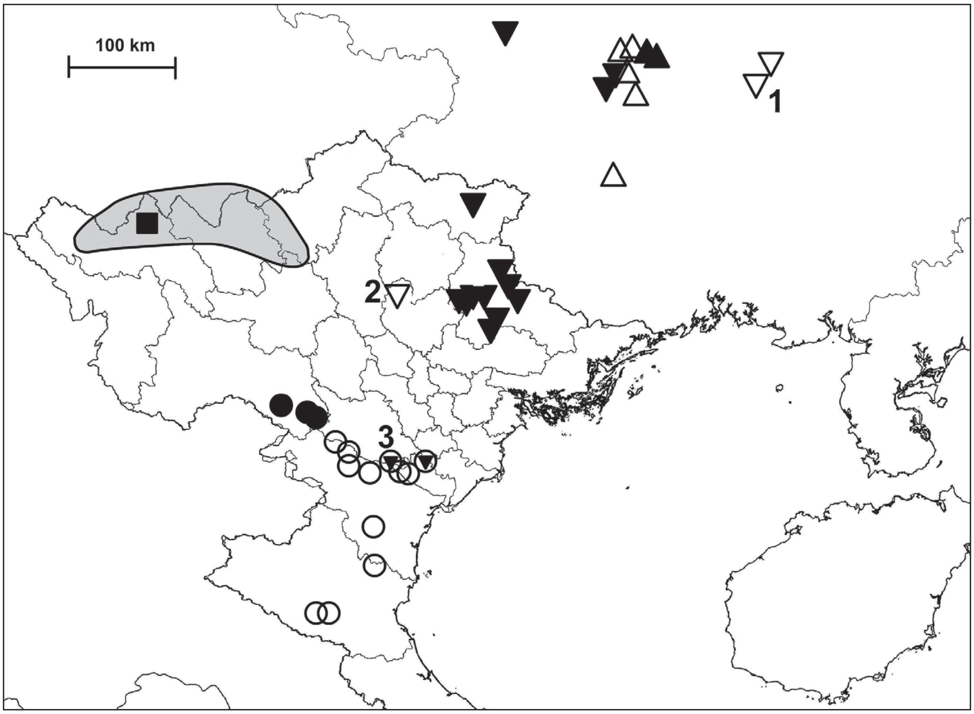

Figure 43. Distribution of *Gudeodiscus* Páll-Gergely, 2013 species. Legends: filled triangle, top down: typical *Gudeodiscus* (*Gudeodiscus*) *phlyarius* (Mabille, 1887), filled triangle, top up: "*Gudeodiscus phlyarius werneri* Páll-Gergely, 2013" (synonym of *phlyarius*); empty triangle, top up: *G.* (*G.*) *phlyarius* populations showing transitional characters towards *werneri* in terms of shell shape; empty triangle, top down: atypical *G.* (*G.*) *phlyarius*; empty circle: *Gudeodiscus messageri raheemi* ssp. n., filled circle: *G.* (*G.*?) *hemmeni* sp. n. (in all localities it co-occurs with *G.* (*G.*) *messageri raheemi* ssp. n.); circle with filled triangle in the middle: co-occurrence of *G.* (*G.*) *messageri raheemi* ssp. n. and atypical *G.* (*G.*) *phlyarius*. The shaded area indicates the area inhabited by *G.* (*G.*) *messageri messageri* (Gude, 1909) and "*anterides*", "*fallax*" and "*gouldingi*"-like populations of *G.* (*G.*) *phlyarius*. Filled square indicates the position of Phong-Tho, the type locality of *Plectopylis verecunda* Gude, 1909 (synonym of *G. phlyarius*). Numbers 1–3 refer to atypical populations assigned to *G.* (*G.*) *phlyarius*. For explanation, see text.

anceyi (Figs 2B, 9G, 11C–F): small size, spiral lines on the ventral surface
cyrtochilus (Figs 2F, 15E–G): small size, thin peristome and callus, no apertural fold
dautzenbergi (Figs 8E–F, 9K–L, 14A–G): shell shape, characteristic aperture and apertural fold, free lower parietal plica absent
emigrans quadrilamellatus (Figs 6F, 13C–D): flat shell, spiral lines
fischeri (Figs 2E, 3A–C, 9P–Q, 15H–N): nautiliform shape (body whorl is conspicuously wider than the previous), blunt callus and apertural fold
francoisi (Figs 7A–C, 13E–K): slowly expanding whorls, characteristic aperture
fruhstorferi (Figs 7D, 9O, 14O–R): few whorls, aperture with thin rim and apertural fold
giardi (Figs 7E–F, 8A, 9I, 13L–U): shell shape, narrow umbilicus, thick peristome

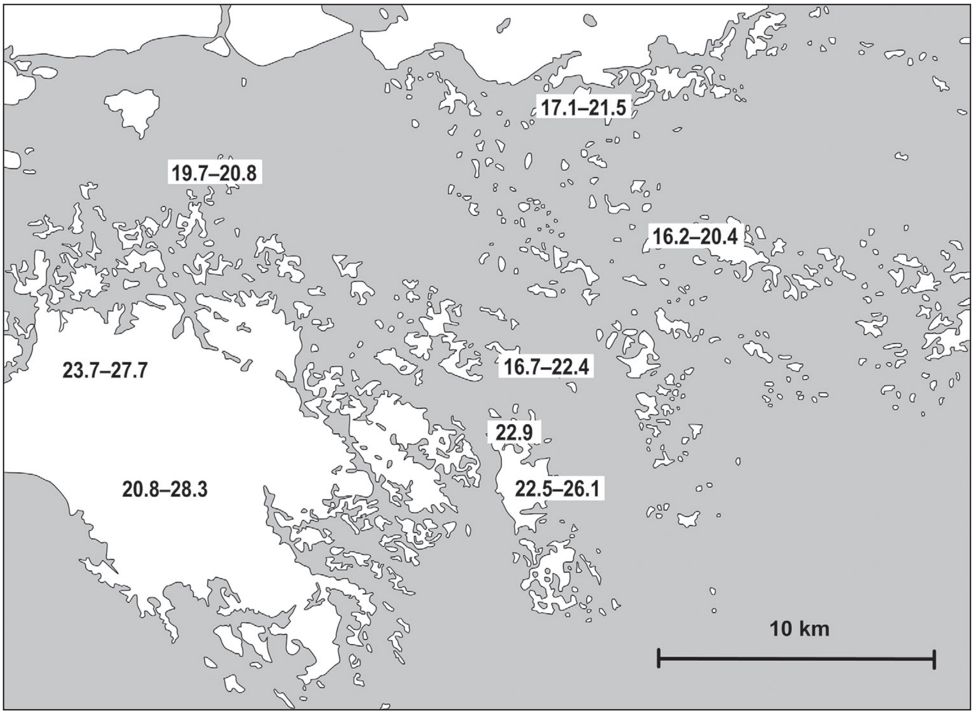

Figure 44. Shell widths of *Halongella schlumbergeri* (mm) in the Halong Bay Area.

hemmeni (Figs 2C–D, 9F, 11G–J): small size, minute apertural fold, characteristic aperture shape

mansuyi (Figs 2A, 9H, 11A–B): small size, glossy ventral surface

messageri messageri (Figs 5F–G, 9E, 12N–Q): slightly elevated spire, callus not angled in the middle, apertural fold always missing

messageri raheemi (Figs 5D, 5E, 10A, 12R–V): body whorl less shouldered than that of the nominotypical subspecies, but plicae have to be observed for correct identification

phlyarius (typical *phlyarius*; Figs 4A–B, 10C–D, 12A–M): characteristic rounded aperture, apertural fold always present

phlyarius (typical *fallax*; Figs 5A, 5C, 10E–F, 11Q–X): flat shell, callus angled in the middle, shell large, nautiliform (body whorl conspicuously wider than *messageri raheemi*)

phlyarius (typical "*anterides*" and "*gouldingi*"; Figs 4–F, 9D, 11K–P): small, flat shell, callus angled in the middle

phlyarius (typical "*verecunda*"; Figs 5B): elevated spire, strong apertural fold

schlumbergeri (Figs 6A–D, 9M–N, 14H–N): robust shell, callus and aperture shape (including the formation of the fold)

suprafilaris (Figs 9A–B, 9R, 14S–Y): narrow umbilicus, solid aperture, sculpture changing suddenly on the body whorl

villedaryi (Figs 8B–D, 9J, 10B, 13V–Y): aperture shaped characteristically, unique keel around the umbilicus in some populations, free lower parietal plica present

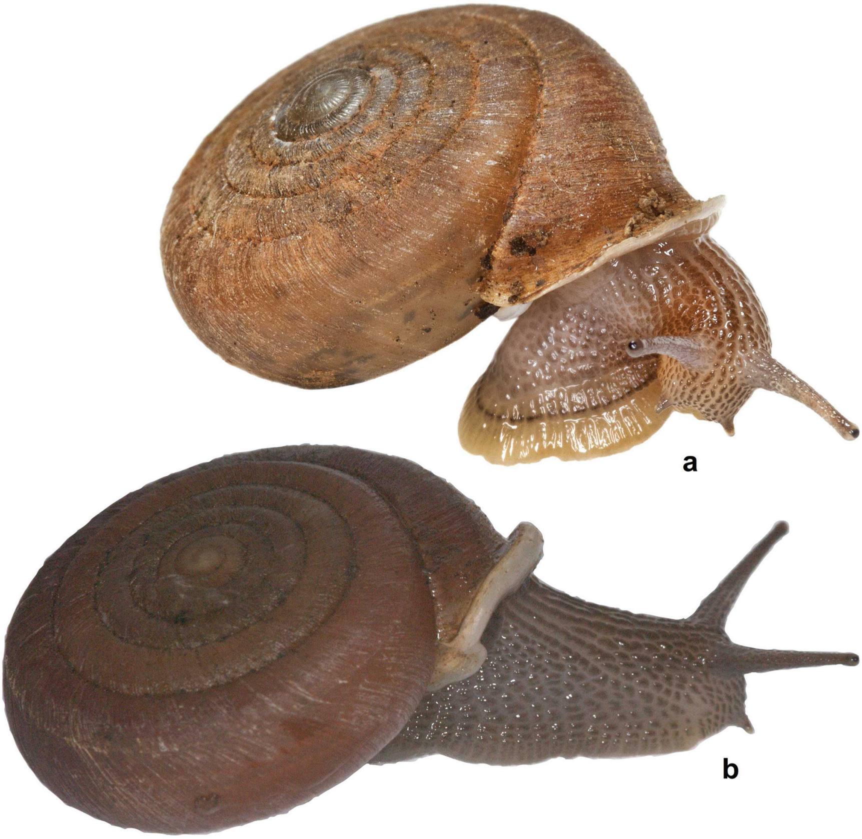

Figure 45. Living specimens of *Gudeodiscus* (*Gudeodiscus*) *giardi giardi* (Fischer, 1898) (**A**), Cao Bằng Province, Hòa An District, Nguyễn Huệ Commune, small hill just outside of Khau Trang Village, 22°33.510'N, 106°10.294'E, leg. Naggs, F. et al. 22.06.2011.; and *Halongella schlumbergeri* (Morlet, 1886) (**B**), Halong Bay area, Vietnam. Photos: F. Naggs.

Identification key to Vietnamese and Chinese plectopylid genera

1	body whorl keeled	**2**
–	body whorl rounded	**3**
2(1)	anterior lamella absent or present as small denticles	***Sinicola***
–	anterior lamella present	***Sicradiscus***
3(1)	shell smaller than 9 mm, smooth at its base, and has a strong apertural fold	***Sicradiscus***
–	shell larger than 9 mm; if it is smaller than 12 mm and smooth, then it has no apertural fold	**4**
4(3)	inner penial wall with distinct pockets standing in 1 or 2 rows	**5**
–	inner penial wall with parallel folds without large pockets	***Halongella***

Table 12. Numbers of specimens examined in each taxon.

taxon	new samples	museum samples	all individuals
anceyi	16	49	1079
cyrtochilus	8	2	71
dautzenbergi	4	38	151
emigrans emigrans	0	2	3
emigrans quadrilamellatus	4	23	68
fischeri	15	14	169
francoisi	6	31	142
fruhstorferi	1	5	37
giardi giardi	21	74	557
hemmeni sp. n.	5	0	38
mansuyi	8	3	351
messageri	0	102	551
messageri raheemi	23	0	152
typical *phlyarius*	34	44	555
phlyarius gouldingi/fallax	2	139	1138
schlumbergeri	28	78	1682
suprafilaris	7	2	102
verecundus	0	6	25
villedaryi	15	19	171
SUM	**197**	**631**	**7042**

5(4) penial retractor simple .... ***Gudeodiscus* (*G.*)**
– penial retractor is covered with additional muscle fibres which attach on the distal end of the penis .... ***Gudeodiscus* (*Veludiscus*)**

Identification key to Vietnamese species (regardless of generic association)

1 shell smaller than 12 mm **2**
– shell larger than 12 mm **5**
2(1) apertural fold well visible **3**
– apertural fold missing or inconspicuous, very weak .... ***cyrtochilus***
3(2) ventral surface smooth, glossy .... ***mansuyi***
– ventral surface sculptured **4**
4(3) free plicae above and below the anterior lamella absent .... ***anceyi***
– upper and lower plicae free from the anterior lamella .... ***hemmeni* sp. n.**
5(1) dorsal reticulate and ventral smooth areas change abruptly .... ***suprafilaris***
– dorsal and ventral sculpture do not change abruptly **6**
6(5) parietal wall with a single lamella **7**
– parietal wall with two lamellae (or the anterior lamella is dissolved into small denticles) **10**

7(6) anterior to the parietal lamella there are four parallel horizontal plicae .... ***e. quadrilamellatus***
– anterior to the lamella there are two horizontal plicae, one above, one below... **8**
8(7) shell about 13–14 mm .... ***fruhstorferi***
– shell larger than 15 mm **9**
9(8) shell strongly-built, seemingly smooth, callus elevated .... ***schlumbergeri***
– shell relatively thin, regularly ribbed, callus weak .... ***e. emigrans***
10(6) shell thin-walled, callus weak, sculpture weak, rather glossy **11**
– shell more strongly-built, callus strong **12**
11(10) shell flat or nearly flat, umbilicus wide .... ***fischeri***
– spire somewhat elevated, umbilicus rather narrow.......................... ***infralevis***
12(10) umbilicus very narrow, dorsal surface domed **13**
– umbilicus moderately narrow, dorsal surface moderately domed **14**
13(12) shell yellowish, callus blunt, rather low .... ***francoisi***
– shell brownish, callus very much elevated, high, rather sharply defined .... ***giardi***
14(12) shell regularly ribbed, rather thin walled **15**
– shell thick walled, strongly built.. **17**
15(14) anterior lamella usually free from the lower plica .... ***phlyarius***
– anterior lamella in contact with the lower plica, or the lower plica is dissolved into denticles **16**
16(15) anterior lamella is in contact with the lower plica, lower plica do not extend beyond the lamella in anterior direction....................... ***messageri messageri***
– anterior lamella dissolved into small denticles; or if not dissolved, the lower plica extends beyond the lamella in anterior direction.................................. .... ***messageri raheemi*** **ssp. n**.
17(14) apertural fold horizontal .... ***schlumbergeri***
– apertural fold oblique **18**
18(17) additional lower plica present under the lamellae .... ***villedaryi***
– additional lower plica absent under the lamellae .... ***dautzenbergi***

Taxonomic positions of the genera *Gudeodiscus*, *Halongella* gen. n., *Sicradiscus* and *Sinicola*

The "Eastern Plectopylidae" (see Páll-Gergely and Hunyadi 2013), namely taxa inhabiting China, Vietnam, Taiwan and Okinawa (Japan) are conchologically relatively diverse. Their common features are the ribbed protoconch and the absence of the long parietal horizontal plica. The genus *Endothyrella*, which mainly inhabits north-eastern India also shares these features with the genera of "Eastern Plectopylidae". Therefore *Endothyrella* is possibly a close relative to the genera *Gudeodiscus*, *Halongella* gen. n., *Sicradiscus* and *Sinicola*. The genera of "Western Plectopylidae" (*Endoplon*, *Chersaecia* and *Plectopylis*) have smooth but matt or "tuberculated" embryonic whorls and usually long horizontal parietal plicae (a main plica and a lower plica) which run to the peristome. Some *Endothyrella* species have long lower and main plicae, but these may not be homologous with those in the *Chersaecia* and *Plectopylis*. Some species which have been assigned to the genus *Chersaecia* (*andersoni* W. Blanford, 1869, *laomontana* L. Pfeiffer, 1863, *oglei*, *serica*, *munipurensis*) also possess ribbed protoconchs. These probably do not belong to any of the genera mentioned herein, and their taxonomic status require revision.

In the revision of the Chinese Plectopylidae (Páll-Gergely and Hunyadi 2013), three genera were recognized, namely *Gudeodiscus*, *Sicradiscus* and *Sinicola*. The most important shell characters for recognition of *Sinicola* are the following: body whorl keeled; periostracal folds usually present on the keel; apertural fold almost always absent; the anterior parietal lamella is absent or present only in some small, separate denticles. *Gudeodiscus* exhibits the following characters: body whorl rounded; periostracal folds absent; apertural fold often present; anterior parietal lamella often present. Both genera inhabit restricted geographical areas with minor overlaps; *Sinicola* ranges from Middle Sichuan to northern Guangxi, Guangdong and eastern Hunan, whereas *Gudeodiscus* ranges from northern Vietnam to southern Hunan and southern Guangdong. Reproductive anatomical investigations (Páll-Gergely and Hunyadi 2013, Páll-Gergely and Asami 2014) found that *Sinicola* species exhibit a ribbed inner penial wall with a few tiny calcareous granules. The ribs are more prominent in the distal part of the penis or continuous until the atrium but this varies between individuals. Examples of *Gudeodiscus* usually also have parallel folds, but they have characteristic small pockets arranged in one or two more or less straight transverse lines in the distal penis. These pockets contain calcareous granules, probably only during the mating period (see discussion on anatomy and biology). The genus *Gudeodiscus* is divided into two groups based on the morphology of the distal penis-penial caecum-retractor muscle complex. In one type, the epiphallus is slender, cylindrical, and addition to the retractor muscle, which attaches on the penile caecum, several muscle fibres attach to the penis itself. In the other type the epiphallus has a somewhat thickened proximal part, and has no additional muscle fibres attached to the penis (Páll-Gergely and Hunyadi 2013, Páll-Gergely and Asami 2014). It may not be legitimate to subdivide the genus on the basis of this anatomical difference, when the shell characters do not show clear distinction (Páll-Gergely and Asami 2014). For example, *G. eroessi* (first type) and *G. multispira* (second type) are conchologically very similar. However, we found that radula traits distinguish between them as well as the genital anatomy does. Therefore we find it well supported to separate these two groups into different subgenera (*Gudeodiscus* and *Veludiscus* subgen. n.).

The taxonomic position of the species classified within *Sicradiscus* is problematic. *Sicradiscus* was erected for several, small bodied species which inhabit a large area ranging from Sichuan to Okinawa, Japan. There is continuous variation across the genus *Sicradiscus* in terms of shell characters. *Sicradiscus invius*, *S. securus*, *S. mansuyi* and *S. feheri* have a rounded body whorl and possess a strong apertural fold. In contrast, *Sicradiscus schistoptychia*, *S. diptychia*, *S. cutisculptus*, *S. ishizakii* and *S. hirasei* have a shouldered body whorl and lack the apertural fold. The two groups are within the same genus because *Sicradiscus transitus* is similar to *S. schistoptychia* in possessing divided palatal plicae and a keeled body whorl, at the same time having a strong apertural fold similar to that of *S. feheri*. Moreover, *S. transitus* ranges between *S. feheri* and *S. schistoptychia* geographically. The present and a previous study (Páll-Gergely and Asami 2014) revealed that the inner morphology of the penis in *S. schistoptychia* is similar to that of *Sinicola*, whereas *S. invius*, *S. mansuyi* and *S. transitus* are similar to *Gudeodiscus* in that trait. Separating some *Sicradiscus* species into *Gudeodiscus* and others in *Sinicola* based on the penial morphology does not resolve their taxonomy because of the large conchological similarity among *Sicradiscus* species. An alternative classification might be to place all *Gudeodiscus*, *Sicradiscus* and *Sinicola* species into one genus because of the transitional features of *Sicradiscus* between *Sinicola* and *Gudeodiscus*. However, our study does not support this because both *Sinicola* and *Gudeodiscus* show clear synapomorphic characters and signs of their separate major radiations in different geographic areas. The most possible explanation is that *Sicradiscus* species represent basal lineages within the *Gudeodiscus–Sicradiscus–Sinicola* complex, in which others diverged into the two lineages, one with the keeled body whorl and folded penial wall and the other with the rounded body whorl and pocketed penial wall. *Sicradiscus* species may probably have undergone only slight conchological changes. This hypothesis is supported by the geographic distribution of most *Sicradiscus* species, roughly between the areas of *Gudeodiscus* and *Sinicola*.

Plectopylis schlumbergeri and *P. fruhstorferi* had parallel folds on the inner penial wall and calcareous granules were found between the parallel folds all along the penis. In both subgenera of the genus *Gudeodiscus* however, the pockets for calcareous granules are arranged in one or two rows, and they are absent elsewhere. Based on this morphological character, they are moved to a new genus, *Halongella*. Additionally, *Halongella* gen. n. species lack a penial caecum, which was found in the majority of *Gudeodiscus* species.

Anatomy and biology

Stoliczka (1871) described the organ proximal to the gametolytic sac of *Plectopylis* as "a shorter, more muscular gland which appears to represent the arrow or amatorial gland". Pilsbry (1894) noted this as "an organ of unknown homology, either a dart sack, a diverticulum of the spermatheca or an appendicula". A spermatophore was found inside this organ of *Gudeodiscus fischeri*. This suggests that the organ is a diverticulum, starting from the wall of the distal end of the vagina/beginning of pedunculus. In most stylommatophoran land snails the diverticulum derives from the stalk of the gametolytic sac. The only exception known before this study was the subfamily Garniierinae (family Clausiliidae), in which the diverticulum derives from the pedunculus (Szekeres 1998).

The inner walls of the male genital organs, especially the penis, show a large diversity across the genera *Gudeodiscus*, *Halongella* gen. n., *Sicradiscus* and *Sinicola*. *Sinicola* and *Halongella* gen. n. have parallel folds on the inner penial wall, occasionally with tiny, usually flat calcareous granules, often without characteristic shapes. The penial wall of *Gudeodiscus* species is usually also characterized by folds, but also pockets arranged in one or two rows in the distal part of the penis. The rows can be straight (e.g. *G. giardi* and *G. villedaryi*), can follow a bell-shaped line (*G. fischeri*), or waves (*G. messageri raheemi* ssp. n.) on the opened penal wall. *Sicradiscus* species have both types of penial sculpture (with and without pockets) (Páll-Gergely and Asami 2014, and this study). In most *Gudeodiscus* specimens the granules are hook or claw-like, and each of them is placed within a pocket on the wall of the head of the penis. Two dissected specimens of *Gudeodiscus phlyarius* (typical *fallax* specimens), however, had flat, oval granules within the penial pockets. It is not clear whether this shape of granules is stable throughout the life span or dependent on season or age. In the revision of the Chinese species (Páll-Gergely and Hunyadi 2013) we described that calcareous hooks are easily removable from the folds in the penial internal wall. In the case of Vietnamese specimens (*G. giardi*, *G. fischeri* and *G. villedaryi*), however, the claws were attached into the wall inside the pocket and were difficult to remove. The SEM images of removed claws revealed that the base of each claw, which was buried into the pocket wall, is granulated in the surface, whereas the exposed tip of each claw was smooth. The hooks from the penis lumen of Chinese *Gudeodiscus phlyarius* (figured specimen in Páll-Gergely and Hunyadi 2013) dissolved with no remains in 90% lactic acid. Thus, these granules may consist of calcium carbonate.

The penial claws or hooks known in other stylommatophoran families (e.g. Zonitidae s.l., Streptaxidae, *Cryptazeca*) do not seasonally disappear and are fixed to the internal wall, because to our knowledge, hook-less specimens have not been reported in contrast to those in Plectopylidae (see also Páll-Gergely and Hunyadi 2013). Those of *Cryptazeca* and Streptaxidae are not calcareous (Visser 1973, Verdcourt 1979, 1985, Gómez 1991), whereas Zonitidae have calcareous claws (Schileyko 2003). The hook-like granules of *Gudeodiscus* and the minute, flat, or sometimes elongated or globular granules of other plectopylid genera may have similar roles but a different origin from the fixed claws of other Stylommatophora.

In some *Gudeodiscus* specimens the proximal (lower) part of the penial wall is ornamented with longitudinal folds only, but in others it has transverse and dense wrinkles (e.g. in *G. giardi giardi* and in one specimen of *G. villedaryi*). The transverse and longitudinal arrangement may result in a reticulated surface of the inner penial wall, such as those in *G. phlyarius* (*fallax*-like specimens). These traits need to be used for taxonomy with careful attention to collection dates and instead may provide opportunities for studies of functional roles for reproductive success for the following reason: two specimens of *G. villedaryi* collected in different periods of the year (20 May and 12 November) from the same locality greatly differed in these traits. The one collected in May was gravid, and its penis had only longitudinal folds on its inner wall, with slightly waved proximal portions of the folds. In contrast, a specimen collected in November was not gravid and had conspicuous, dense and transversal folds on the proximal portion of the inner wall of the penis. This transversal folded structure turned suddenly to a longitudinal folded area with calcareous claws between the pockets. This result suggests that the morphology of fine sculpture of the inner penial wall (at least inside the proximal half of the penis) may be seasonally variable. The gravid individual may have lost hooks in a mating period before collected in May. The latter individual with no embryo may have been in a period for copulation. Our observation suggests that the penial internal wall may be restructured to regenerate the hook-like calcareous claws for copulation. Further studies are necessary to test this hypothesis.

The other organs of male genitalia, penial caecum and epiphallus have generally a simpler inner surface, usually with parallel and longitudinal folds, than the penis. In smaller species it is difficult to open these very slim organs, especially the epiphallus. The longitudinal folds on the inner wall of the epiphallus of *Halongella* gen. n. species have perpendicular projections which overlap with those of the neighbouring fold. Besides this, all other species have an epiphallus with simple internal longitudinal folds. The inner wall of the penial caecum is also ornamented by longitudinal folds, which are sometimes wavy, and form hollows with the neighbouring fold. This structure is similar to the penial sculpture of *Sinicola* species. A function of these hollows would probably be to hold the small calcareous granules. In some species the sculpture of the penial caecum is more complex; *Gudeodiscus messageri raheemi* has deep sinuses with the calcareous granules. *Gudeodiscus giardi giardi* has pockets formed by two neighbouring papillae (Páll-Gergely and Asami 2014). The calcareous granule within the caecum can be elongated or globular without any characteristic shape, such as in one of the dissected *G. messageri raheemi* specimens, or the granules can be hook-like, similar to, but smaller than those found in the penial lumen, such as in a specimen of *G. pulvinaris pulvinaris* (see Páll-Gergely and Asami 2014).

Specimens that were fixed in 70% ethanol were used for this investigation. Thus, at this stage of study, we are not able to rule out a possibility that some of the granules appeared as observed because of the process of preservation. However, hook structure corresponds to pocket structure in the penial internal surface. Each hook is regularly located in a pocket in a determined orientation. Further, they exhibit a taxonomically characteristic and sophisticated shape. For these reasons, the presence of hooks and granules in the present family cannot be ascribed to an artefact during preservation.

The absence of embryos in the uterus was statistically significantly associated with the presence of calcareous granules inside the penis, within *Gudeodiscus* ($p = 0.0001$) and also across all the four genera ($p = 0.0006$) (Tables 3–5). This strongly suggests that these granules may function as a disposable male mating apparatus. These granules disappear perhaps through repeated copulation in a mating season. It could require some time to gain the granules again if they lose granules and bear offspring. Thus, for some time during the mating season, they might remain with no granules before embryos develop. If so, these would exhibit no granules or embryos. However, this was the case only in three of 34 specimens examined in this study. Our results illuminate the importance of further studies on their reproductive life history and the ecological function of these granules.

The function of the calcareous hooks and granules inside the penis are unknown, although they probably play some role as a mating apparatus as well as the noncalcareous hooks in other groups. It has been classically postulated that these may function for mechanical stimulation for mating success like other penial structures or darts (Tompa 1984; Atkinson and Atkinson 1987). However, later studies have shown that love darts are not for physical stimulation but to inject mucus which includes a substance that increases paternity by inducing reconfiguration of partner's organs for spermatophore digestion (Koene and Chase 1998; Chase and Blanchard 2006; Kimura et al. 2014). Separately, De Winter et al. (1999) proposed that the spines on the penial wall play a role in the process of spermatophore formation in the streptaxid genus *Sinistrexcisa*. This is probably not the case in Plectopylidae, because they have the structurally distinguishable epiphallus. Their spermatophores are formed in this organ instead of the penis, and thus the structure of parallel inner folds in the epiphallus matches the morphology of spermatophore. Tompa (1984) also suggested that the penial hooks may function as mechanical holdfasts during mating. The present study provides a systematic ground for further studies on the evolution of mating apparatus inside the penis.

The function of the characteristic vaginal granules in one of the *Halongella schlumbergeri* specimens are also unknown. To our knowledge, no disposable granules have been reported in land snails which are attached to the vagina wall. The presence of vaginal granules in a non-gravid specimen and the presence of "vaginal sand" in a gravid specimen indicate that these granules are present only seasonally, probably related to the mating period. The characteristic shape of the granules, namely the flat base portion and the needle-bearing apical part does not support the hypothesis that they are artefacts formed during preservation.

To our knowledge, information on plectopylid radulae was published by Stoliczka (1871; *Plectopylis achatina*, *P. cyclaspis* and *Endothyrella pinacis*), Solem (1966; *Chersaecia simplex*) and Chang and Ookubo (1999; *Sicradiscus ishizakii*). Here we publish the radula morphology of 23 Chinese and Vietnamese species. Our limited information suggests that the relative size of the central tooth and the shape of the marginal teeth may be used in the systematics of the family. The genera *Sicradiscus*, *Sinicola* and the subgenus *Gudeodiscus* have relatively large central tooth (as large as or larger than the ectocone of the first laterals), and their marginal teeth are tricuspid with pointed cusps and deep incision between the cusps. In contrast, *Plectopylis*, *Halongella* gen. n., and *Gudeodiscus* (*Veludiscus*) subgen. n. possess smaller central tooth than the ectocone of the first lateral, and their marginals are bicuspid, or even if they are tricuspid, the innermost cusp is blunt and small, and there is a shallow incision between the inner two cusps. Stoliczka (1871) mentioned that *Endothyrella pinacis* (that time *Plectopylis pinacis*) has a larger central tooth than the two *Plectopylis* species, but did not provide a description or drawing of the marginal teeth. The description of the radula of *Chersaecia simplex* by Solem (1966) is accurate but he did not publish drawings. In that species, the central tooth is "tiny", supposedly smaller than the ectocones of the first laterals. The ectocones of the outer marginals are "reduced and split" (= marginals are tricuspid). This information on the marginals, however, is insufficient to allow comparison with our data.

Habitat

Plectopylid species seem to be associated with calcareous areas. Living specimens occur at the base of large limestone rocks surrounded by leaf litter and humus. Thus, they are not rock-dwelling but ground-dwelling. Most living species have reticulated sculpture on the dorsal shell side, which is often covered with soil and this may be of value in providing camouflage.

Geographical coverage of the Vietnamese plectopylid fauna

At the beginning of the 20th Century all the available information on the distribution and taxonomy of Plectopylidae came with specimens from northern and eastern part of northern Vietnam (Tonkin) (Figure 39). We were able to examine only a few newly collected northern Tonkinese samples. Therefore, our knowledge on those species reported from the northern border region of Vietnam is mainly based on museum specimens. On the other hand, we examined several newly collected samples from the eastern part of northern Vietnam (Tonkin). Almost all of these specimens were identified to hitherto known species. Most of these species were found in several localities. Thus, this study covered the taxonomic diversity of plectopylids in the eastern Tonkinese area relatively well. Plectopylid specimens from western Tonkin have been examined for the first time. This resulted in the present description of a new species and a new subspecies.

Little information on plectopylid diversity has been obtained in the lowlands of the Red River, although these areas may not provide suitable habitats for land snails that prefer limestone outcrops or mountainous areas. Molluscan fauna in the border region of Sơn La and Yên Bái Provinces (Phan Xi Păng= “Farsipan” Mountain and its vicinity) is nearly unknown, maybe due to their high abundance in the limestone-free bedrock. Humid mountain forests there, however, may provide suitable habitats for plectopylids.

The southernmost Vietnamese county where plectopylids have been recorded is Nghệ An. The southern part of Vietnam may have been less intensively studied than the northern area (Tonkin). Accordingly the southernmost distribution of the family remains undetermined.

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References

Ancey C-F (1885) Novelles Contributions Malacologiques. Sur divers Mollusques de l'Empire Chinois. Bulletins de la Société Malacologique de France 2: 113–137. http://www.biodiversitylibrary.org/item/54639#page/135/mode/1up

Ancey C-F (1888) Mollusques du Haut-Tonkin (Récoltes de M. Villedary). Le Naturaliste: journal des échanges et des nouvelles 2(10): 70–72. http://www.biodiversitylibrary.org/item/39886#page/74/mode/1up

Atkinson JW, Atkinson KEH (1987) "Crystals" in the penis of land snails of the genus *Anguispira*: energy dispersive X-ray microanalysis with scanning electron microscopy. Transactions of the American Microscopical Society 106: 126–133. doi: 10.2307/3226309

Benson WH (1863) Characters of new Land-Shells from the Andaman Islands, Burmah, and Ceylon, and of the Animal of Sophina. Annals and Magazine of Natural History 3(11): 318–323. http://www.biodiversitylibrary.org/item/53370#page/334/mode/1up

Blanford WT (1865) Contribution to Indian Malacology, No. V. Descriptions of new land shells from Arakan, Pegu, and Ava ; with notes on the distribution of described species. Journal of the Asiatic Society of Bengal 34(2): 66–105. http://www.biodiversitylibrary.org/item/114408#page/146/mode/1up

Blanford WT (1869) Descriptions of new Land and Freshwater Mollusc Species collected by Dr. John Anderson in Upper Burma and Yunan. Proceedings of the Zoological Society of London 27: 444–450. http://www.biodiversitylibrary.org/item/91102#page/539/mode/1up

Bouchet P, Rocroi J-P (2005) Classification and Nomenclator of Gastropod Families. Malacologia 47(1–2): 1–397. http://www.biodiversitylibrary.org/page/25127194#page/11/mode/1up

Chang KM, Ookubo K (1999) Anatomy and Systematics on *Plectopylis* (*Sinicola*) *ishizakii* Kuroda, 1941 from Taiwan. Bulletin of Malacology (Taiwan ROC) 23: 21–28.

Chase R, Blanchard KC (2006) The snail's love-dart delivers mucus to increase paternity. Proceedings of the Royal Society of London B, Biological Sciences 273(1593): 1471–1475. doi: 10.1098/rspb.2006.3474

Dautzenberg P, Fischer H (1905a) Liste des Mollusques récoltés par M. le Capitaine de Frégate Blaise, et description d'espèces nouvelles. Journal de Conchyliologie 53: 85–234. http://www.biodiversitylibrary.org/item/55051#page/101/mode/1up

Dautzenberg P, Fischer H (1905b) Liste des Mollusques Récoltés par M. H. Mansuy en Indo-Chine et au Yunnan et Description d'Espèces Nouvelles. Journal de Conchyliologie 53: 343–371. http://www.biodiversitylibrary.org/item/55051#page/379/mode/1up

Dautzenberg P, Fischer H (1908) Liste des mollusques récoltés par M. Mansuy en Indo-Chine et description d'espèces nouvelles. Journal de Conchyliologie 56: 169–217. http://www.biodiversitylibrary.org/item/55061#page/195/mode/1up

De Winter AJ, Gomez BJ, Prieto CE (1999) *Sinistrexcisa*, a New Genus of Land Snail from Central West Africa with Four New Species (Gastropoda: Pulmonata: Streptaxidae). Journal of Molluscan Studies 65(2): 209–221. doi: 10.1093/mollus/65.2.209

Degner E (1923) Zur Anatomie und systematischen Stellung von *Sculptaria* Pfeiffer. Archiv für Molluskenkunde 55(4): 14–160.

Fischer H (1898a) Notes sur la Faune du Haut-Tonkin V. Description d'une Espèce Nouvelle de *Plectopylis*. Bulletin Biologique de la France et de la Belgique 28: 310–338. http://www.biodiversitylibrary.org/item/40690#page/326/mode/1up

Fischer H (1898b) Description d'une espéce nouvelle de *Plectopylis*. Journal de Conchyliologie 46: 214–218. http://www.biodiversitylibrary.org/item/54071#page/220/mode/1up

Fischer H (1899) Description d'une espéce nouvelle de *Plectopylis*. Bulletin biologique de la France et de la Belgique 32: 329–332. http://www.biodiversitylibrary.org/item/40660#page/341/mode/1up

Fischer H, Dautzenberg P (1904) Catalogue des mollusques terrestres et fluviatiles de l'Indo-Chine orientale cites jusqu'à ce jour. Mission Pavie, Etudes diverses 3: 390–442.

Godwin-Austen HH (1875) Descriptions of five new Species of *Helicidae* of the Subgenus *Plectopylis*, with remarks on all the other known forms. Proceedings of the Zoological Society of London, 608–614. http://www.biodiversitylibrary.org/item/90419#page/780/mode/1up

Godwin-Austen HH (1879) On new species of the Genus *Plectopylis* of the Family Helicidae. Journal of the Asiatic Society of Bengal 48(2): 1–4. http://www.biodiversitylibrary.org/item/129159#page/371/mode/1up

Gómez BJ (1991) Morphological and histological study of the genital ducts of *Cryptazeca monodonta* (Pulmonata, Orthurethra), with special emphasis on the auxiliary copulatory organ. Zoomorphology 111: 95–102. doi: 10.1007/BF01632875

Gould AA (1847) [Dr. Gould described new shells…]. Proceedings of the Boston Society of Natural History 2: 218–221. http://www.biodiversitylibrary.org/item/37031#page/226/mode/1up

Gude GK (1897a) Armature of Helicoid landshells and new forms of *Plectopylis*. Science Gossip 3: 332. http://www.biodiversitylibrary.org/bibliography/49978#/summary

Gude GK (1897b) Armature of Helicoid landshells. Science Gossip 4: 138–139. http://www.biodiversitylibrary.org/bibliography/49978#/summary

Gude GK (1899a) Armature of Helicoid landshells. And new forms of *Plectopylis*. Science Gossip 5: 332–333. http://www.biodiversitylibrary.org/bibliography/49978#/summary

Gude GK (1899b) Armature of Helicoid landshells. And new species of *Plectopylis*. Science Gossip 6: 75–77. http://www.biodiversitylibrary.org/bibliography/49978#/summary

Gude GK (1899c) Armature of Helicoid landshells and new sections of *Plectopylis*. Science Gossip 6: 147–149. http://www.biodiversitylibrary.org/bibliography/49978#/summary

Gude GK (1899d) Armature of Helicoid landshells. Science Gossip 6: 174–177. http://www.biodiversitylibrary.org/bibliography/49978#/summary

Gude GK (1900) Description of a new species of *Plectopylis* from Tonkin. The Annals and Magazine of Natural History 7(5): 313. doi: 10.1080/00222930008678289, http://www.biodiversitylibrary.org/item/55143#page/329/mode/1up

Gude GK (1901a) Sur une collection de *Plectopylis* du Tonkin, avec la description de six espèces nouvelles. Journal de Conchyliologie 49: 197–212. http://www.biodiversitylibrary.org/item/53864#page/209/mode/1up

Gude GK (1901b) Notes on some known species of *Plectopylis* and description of a new variety of Plectopylis plectostoma, Bens. Journal of Malacology 8: 46–49. http://www.biodiversitylibrary.org/item/89648#page/65/mode/1up

Gude GK (1901c) On two new and three hitherto unfigured species of *Plectopylis* from Tonkin. Journal of Malacology 8: 110–117. http://www.biodiversitylibrary.org/item/89648#page/142/mode/1up

Gude GK (1908) Observation on a number of *Plectopylis* collected in Tonkin by M. Mansuy with description of four new species. Journal de Conchyliologie 55: 345–357.

Gude GK (1909) Descriptions of six new species of *Plectopylis* from Tonkin. Proceedings of the Malacological Society of London 8: 213–218. http://www.biodiversitylibrary.org/item/55052#page/381/mode/1up

Gude GK (1911) Note on some preoccupied Molluscan generic names and proposed new genera of the family Zonitidae. Proceedings of the Malacological Society of London 9: 269–273. http://www.biodiversitylibrary.org/item/96830#page/309/mode/1up

Gude GK (1914) The Fauna of British India including Ceylon and Burma. Mollusca.–II. (Trochomorphidae--Janellidae). Taylor and Francis, London, 520 pp. http://www.biodiversitylibrary.org/item/46617#page/5/mode/1up

Gude GK (1915) XL. Mollusca: IV: Helicidae. Genus *Plectopylis*. Records of the Indian Museum 8: 505–513. http://www.biodiversitylibrary.org/item/41753#page/700/mode/1up

Haas F (1933) Zur Systematik der chinesischen "Helicodonten". Archiv für Molluskenkunde 65(4–5): 230–231.

Heude RPM (1882) Mémoires concernant l'histoire naturelle de l'empire chinois par des pères de la Compagnie de Jésus. Notes sur les Mollusques terrestres de la vallée du Fleuve Bleu II, Mission Catholique, Chang-Hai, 1–88. http://www.biodiversitylibrary.org/bibliography/50365#/summary

Heude RPM (1885) Mémoires concernant l'histoire naturelle de l'empire chinois par des pères de la Compagnie de Jésus. Notes sur les Mollusques terrestres de la vallée du Fleuve Bleu III, Mission Catholique, Chang-Hai, 89–132. http://www.biodiversitylibrary.org/bibliography/50365#/summary

Jaeckel SH (1950) Die Mollusken eines tropischen Flußgenistes aus Tonkin. Archiv für Molluskenkunde 79: 15–20.

Kerney MP, Cameron RAD (1979) A Field Guide to the Land Snails of Britain and Northwest Europe. Collins, London, 288 pp.

Kimura K, Chiba S, Koene JM (2014) Common effect of the mucus transferred during mating in two dart-shooting snail species from different families. Journal of Experimental Biology 217: 1150–1153. doi: 10.1242/jeb.095935

Koene JM, Chase R (1998) The love dart of *Helix aspersa* Müller is not a gift of calcium. Journal of Molluscan Studies 64: 75–80. http://mollus.oxfordjournals.org/content/64/1/75.short

Kuroda T (1941) A Catalogue of Molluscan Shells from Taiwan (Formosa), with Description of New Species. Memoirs of the Faculty of Science and Agriculture (Taihoku Imperial University) 22: 65–216.

Mabille MJ (1887a) Molluscorum Tonkinorum diagnoses. Masson, Paris, 18 pp.

Mabille MJ (1887b) Sur Quelques Mollusques du Tonkin. Bulletins de la Société Malacologique de France 4: 73–164. http://www.biodiversitylibrary.org/item/54677#page/83/mode/1up

Martens E von (1875) Bemerkungen zu vorstehender Arbeit. Jahrbücher der Deutschen Malakozoologischen Gesellschaft 2: 126–135. http://www.biodiversitylibrary.org/item/86730#page/142/mode/1up

Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York, 334 pp.

Möllendorff OF von (1886) Materialen zur Fauna for China. Jahrbücher der Deutschen Malakozoologischen Gesellschaft 13: 156–210. http://www.biodiversitylibrary.org/item/55191#page/168/mode/1up

Möllendorff O von (1901) Diagnosen neuer von H. Fruhstorfer in Tongking gesammelter Landschnecken. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 33(5–6): 65–81, 110–119. http://www.biodiversitylibrary.org/item/53275#page/275/mode/1up

Morlet L (1886a) Liste des Conquilles recueillies, au Tonkin, par M. Jourdy, chef d'escardon d' artillerie, et description d'espèces nouvelles. Journal de Conchyliologie 34: 257–295. http://www.biodiversitylibrary.org/item/54516#page/265/mode/1up

Morlet L (1886b) Diagnoses de mollusques terrestres et fluviatiles du Tonkin, 1–7. http://www.biodiversitylibrary.org/item/51561#page/5/mode/1up

Páll-Gergely B, Hunyadi A (2013) The family Plectopylidae Möllendorff 1898 in China (Gastropoda, Pulmonata). Archiv für Molluskenkunde 142(1): 1–66. http://www.ingentaconnect.com/content/schweiz/afmijm/2013/00000142/00000001/art00001

Páll-Gergely B, Asami T (2014) Additional information on the distribution, anatomy and systematics of living and fossil Chinese Plectopylidae (Gastropoda: Pulmonata). Genus 25(3): 527–564.

Pfeiffer L (1863) Novitates Conchologicae, Series prima. Mollusca extramarina. Descriptions et figures de coquilles, estramarines nouvelle, ou peu connues. Beschreibung and Abbildung neuer oder kritischer Land- and Süsswasser Mollusken. T. Fischer, Cassel, Germany, 2: 139–303.

Pilsbry HA (1893) Manual of Conchology; Structural and Systematic. With illustrations of the Species. Second series: Pulmonata, Vol. 8., I-LVIII, Conchological Section, Academy of Natural Sciences, Philadelphia, 297 pp. http://www.biodiversitylibrary.org/item/16712#page/9/mode/1up

Pilsbry HA (1894) Manual of Conchology. Second Series: Pulmonata, Vol 9. Academy of Natural Sciences Philadelphia, Philadelphia, 49–160. http://www.biodiversitylibrary.org/item/16303#page/9/mode/1up

Pilsbry HA (1904) *Plectopylis* in the Riukiu Islands. The Nautilus 18: 58–59. http://www.biodiversitylibrary.org/item/17975#page/76/mode/1up

Pilsbry HA (1905) Anatomical and systematic notes on *Dorcasia*, *Trigonephrus*, gen. n., *Corilla*, *Thersites*, and *Chloritis*. Proceedings of the Malacological Society of London 6: 286–291. http://www.biodiversitylibrary.org/item/52315#page/332/mode/1up

Raheem DC, Taylor H, Ablett J, Preece RC, Aravind NA, Naggs F (2014) A Systematic Revision of the Land Snails of the Western Ghats of India. Tropical Natural History Supplement 4(1–13): 1–285.

Schileyko AA (1998) Treatise on Recent Terrestrial Pulmonate Molluscs, Part 1. Achatinellidae, Amastridae, Orculidae, Strobilopsidae, Spelaeodiscidae, Valloniidae, Cochlicopidae, Pupillidae, Chondrinidae, Pyramidulidae. Ruthenica (Supplement) 2: 1–127.

Schileyko AA (1999) Treatise on Recent Terrestrial Pulmonate Molluscs, Part 4. Draparnaudiidae, Caryodidae, Macrocyclidae, Acavidae, Clavatoridae, Dorcasiidae, Sculptariidae, Corillidae, Plectopylidae, Megalobulimulidae, Strophocheilidae, Cerionidae, Achatinidae, Subulinidae, Glessulidae, Micractaeonidae, Ferrussaciidae. Ruthenica (Supplement) 2: 435–564.

Schileyko AA (2001) Treatise on Recent Terrestrial Pulmonate Molluscs, Part 7. Endodontidae, Thyrophorellidae, Charopidae. Ruthenica (Supplement) 2: 881–1034.

Schileyko AA (2003) Treatise on recent terrestrial pulmonate mollusks. 10. Ariophantidae, Ostracolethaidae, Ryssotidae, Milacidae, Dyakiidae, Staffordiidae, Gastrodontidae, Zonitidae, Daudebardiidae, Parmacellidae. Ruthenica (Supplement) 2: 1309–1466.

Schileyko AA (2010) A redescription of *Ruthvenia biciliata* (L. Pfeiffer, 1855), with revised generic diagnosis for *Ruthvenia* Gude, 1911 (Gastropoda: Pulmonata: Charopidae). Annalen des Naturhistorischen Museums in Wien (Serie B) 111: 13–18. http://www.jstor.org/stable/41767446

Schileyko AA (2011) Check-list of land pulmonate molluscs of Vietnam (Gastropoda: Stylommatophora). Ruthenica 21(1): 1–68. http://www.ruthenica.com/documents/vol21_Schileyko_1–68.pdf

Solem A (1966) Some non-marine mollusks from Thailand, with notes on classification of the Helicarionidae. Spolia Zoologica Musei Hauniensis 24: 1–110.

Solem A (1968) "*Ptychodon*" *misoolensis* Adam and Van Benthem Jutting, 1939, A New Guinea *Strobilopsis* land snail and review of the genus *Enteroplax*. Veliger 11: 24–30.

Stoliczka F (1871) Notes on Terrestrial Mollusca from the Neighbourhood of Moulmein (Tenasserim provinces), with Description of New Species. Journal of the Asiatic Society of Bengal 40(2): 217–223.

Szekeres M (1998) The systematic position of the *Garnieria* and *Tripychia* groups, two ambiguous phylogenetic branches of Clausiliidae (Gastropoda Pulmonata). Basteria 62: 175–179.

Thanh ĐN (2008) Tình hình và kết quả điều tra thành phần loài ốc ở cạn ở Việt Nam hiện nay (Overview on the species composition of the landsnails fauna of Vietnam). Sinh Hoc Journal of Biology 30(4): 1–15. [In Vietnamese]

Tompa A (1984) Land snails (Stylommatophora). In: Wilbur KM (Ed.) The Mollusca, vol VII: Reproduction. Academic Press, London, 47–140.

Tryon GW (1887) Manual of Conchology; Structural and Systematic. With Illustrations of the Species. Second series: Pulmonata. – Volume III. Helicidae, Volume I. Published by the Author, Philadelphia, 313 pp. http://www.biodiversitylibrary.org/item/16713#page/9/mode/1up

Yen T-C (1939) Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt am Main, 234 pp.

Verdcourt A (1979) The identity of the European greenhouse *Gulella* (Pulmonata: Streptaxidae). Journal of Conchology 30: 101–104. http://www.conchsoc.org/node/5079

Verdcourt B (1985) New taxa of *Gulella* L. PFR and *Ptychotrema* Mörch (Mollusca, Streptaxidae) from eastern Africa. Journal of Conchology 32: 109–121. http://www.conchsoc.org/resources/show-abstract-32.php%3Fid%3D364

Visser M (1973) The ontogeny of the reproductive system of *Gonaxis gwandaensis* (Preston) (Pulmonata, Streptaxidae) with special reference to the phylogeny of the spermatic conduits of the pulmonata. Annals of the University of Stellenbosch, Seria A 48(4): 9.

Zilch A (1959–1960) Handbuch der Paleozoologie – 6(2) Euthyneura. Gebrüder Borntraeger, Berlin, 481–834.

Supplementary material 1

Exact locality data of Vietnamese Plectopylidae species.

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Data type: Table.

Explanation note: This Excel file contains all exact locality data of Vietnamese Plectopylidae. The localities are subdivided into three columns (verbal description of the locality; latitude; longitude).

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Distribution of *Benthesicymus tanneri* Faxon, 1893 (Dendrobranchiata, Benthesicymidae) off the west coast of Mexico and notes on its morphology

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Abstract

A large series of specimens of *Benthesicymus tanneri* Faxon, 1893 (Dendrobranchiata; Benthesicymidae) was collected during an extensive survey of deep-water invertebrate fauna off western Mexico. In total, 61 males and 122 females (M:F ratio = 1:2) from 44 sampling stations were examined, considerably increasing the number of known specimens and sampling localities for this species which is widely distributed along the Pacific coast of Mexico. The collection is the largest available for this species to date and presents first records from off the west coast of the Baja California Peninsula and a slight increase of the northernmost record within the Gulf of California. On the whole, females grew larger than males. The petasma of males of different sizes and the female thelycum of *B. tanneri* are illustrated. The petasma of *B. tanneri* presents a ventrolateral crescent-shape process otherwide found only in *B. tirmiziae* Crosnier, 1978 and in *B. bartletti* S.I. Smith, 1882. A key to the four species of *Benthesicymus* presently known from the eastern Pacific is presented.

Keywords

Benthesicymus tanneri, eastern Pacific, distribution, key to species

Introduction

Benthesicymidae is a relatively large family of shrimps that contains 39 species within five genera. The most species-rich genera are *Gennadas* (16 species) and *Benthesicymus* (15 species) (De Grave and Fransen 2011). The genus *Benthesicymus* was first reviewed by Burkenroad (1936) when the group comprised 19 species. However, since then several of those species have been considered junior synonyms or assigned to different genera, and three new species have been described (see De Grave and Fransen 2011). Burkenroad (1936) separated the 19 species known at that time into two groups (Groups I and II) taking into consideration a long series of characters, including the shape of the exopod of the first maxilliped, the merus of the second maxilliped and the dactyl of the third maxilliped, the relative size of the exopodite of the pereiopods, the position of the pterygostomial spine, and the shape of the pterygostomial carina. In addition, he also considered the structure of the petasma and thelycum. According to Burkenroad (1936), the type species of *Benthesicymus*, *B. crenatus* Spence Bate, 1881, is part of Group I. The two groups (I and II) are essentially the same as those referred to by Kikuchi and Nemoto (1991) and Dall (2001), but these authors used a reduced series of characters and an updated list of species. Kikuchi and Nemoto (1991), however, ommitted *B. cereus* Burkenroad, 1936, from their list and key, and included *B. longipes* Bouvier, 1906 (now synonymized with *B. iridescens* Spence Bate, 1881) and *B. brevirostris* Kikuchi & Nemoto, 1991 (now transferred to the genus *Altelatipes*). Dall (2001) cited the 15 species from the Indo-West Pacific known to him, including *B. brevirostris* and *B. longipes*, and provided a key to species from that region.

Characters used by Kikuchi and Nemoto (1991) in their definition of Group I and II included the position of the branchiostegal spine, the shape of the second maxilliped and of the dactylus of third maxilliped, and the relative size of pereiopods' exopod. Their Group II includes five species, two of which have been recorded in deep waters of the Mexican Pacific: *B. altus* Spence Bate, 1881, and *B. tanneri* Faxon, 1893 (see Hendrickx 1996). Although similar in their general shape, *B. altus* and *B. tanneri* are easy to separate based on the structure of the thelycum and petasma. Kikuchi and Nemoto's (1991) Group I included 10 species, one of them also reported off western Mexico, *B. laciniatus* Rathbun, 1906, which distinctively features small spines on the posterolateral margin of the fifth abdominal somite.

To date, four species have been certainly recorded in the eastern Pacific. *Benthesicymus altus* is distributed from California, USA, to the Galapagos Islands, but it also occurs in the Atlantic and Indo-Pacific (Guzmán and Wicksten 2000). *Benthesicymus tanneri* is known from California, USA, and the Gulf of California (north to 27°34'N; 110°53'W), Mexico, to Chile (21°19'S) (Retamal and Soto 1993; Wicksten and Hendrickx 2003). The taxonomic status of *B. laciniatus* Rathbun, 1906, was reviewed by Wicksten (2004) and this species is known from Hawaii, Santa Catalina Island (as *Gennadas pectinatus* Schmitt, 1921, a junior synonym of *B. laciniatus*), California, USA, and off Baja California Peninsula (31°20'N; 120°8'W) (Wicksten 2004). Another species of Group II, *B. investigatoris* Alcock & Anderson, 1899, is widely distributed in the world oceans and has been reported in the eastern Pacific off Chile (Salas y Gómez Island and Ridge; Nazca Ridge) by Retamal and Moyano (2010). There is an additional record for a fifth species of *Benthesicymus* in the eastern Pacific, *B. crenatus*, but this record is based on a tentative identification by I. Peréz-Farfante ("*Benthesicymus* cf. *crenulatus*", USNM 216490) from a specimen collected next to the Cortés Bank (32°08'N; 120°48'W; 3782 m depth) and it is doubtful considering that all records for *B. crenatus* are in the northwestern and central Pacific Ocean (Jamieson et al. 2009).

Benthesicymus tanneri is a moderate large species, with females reaching up to 99 mm total length (Hendrickx 1996) and a maximum known size of 112 mm (Faxon 1893). Material examined by Faxon (1893) was collected in 22 "Albatross" stations, from off Ecuador (3°56'N; 81°40'15"W) to the Central Gulf of California (27°34'N; 110°53'40"W), in a depth range from 385 to 1322 fathoms (ca 704–2,427 m depth). Because it is a deep-water species, records after those presented by Faxon (1893, 1895) are scarce and several authors have only repeated previous literature records or geographic distribution (e.g., Schmitt 1921, Rodríguez de la Cruz 1987, Wicksten 1989, Wicksten and Hendrickx 1992, 2003, Hendrickx 1993, 1995, Guzmán and Wicksten 2000). Rathbun (1904: 147) was the first to report on additional material collected by the "Albatross" off San Diego, within the Gulf of California, and off Ecuador, including the Galapagos Islands (Sts. 2923, 2929, 3009, 3010, 2792, 2793, 2808, 2818; from 331 to 1322 fathoms). In her monograph on shrimp from Peru, Méndez (1981: 31) included a large series of samples collected from a very wide latitudinal range (i.e., 3°31'S to 18°17'S) between 500 and 1300 m depth. Kameya et al. (1997) reported *B. tanneri* in three stations off Peru, Retamal and Jara (2002) cited it from off Chile, and Cornejo-Antepara (2010) from off Ecuador. It is also known from off Costa Rica (Vargas and Wehrtmann 2009) and off El Salvador (J. López, pers. comm.).

Material collected in Mexican waters during the TALUD cruises III-VII (1991–2001) in the SE Gulf of California was reported by Hendrickx (2001) and Hendrickx (2004; distribution maps), adding many new records and increasing the known distribution range of this species. A large series of specimens, however, was collected during subsequent research cruises off the Pacific coast of Mexico and has not yet been reported. This series is included herein. This contribution provides and updated distribution of *B. tanneri* for the Mexican Pacific and new data related to the petasma and thelycum of this species. Additionally, a taxonomic key for the species occurring in the American Pacific is provided.

Material and methods

The material on which this study is based was collected by the R/V "El Puma" of the Universidad Nacional Autónoma de México (UNAM), between 1991 and 2014. Specimens of *Benthesicymus tanneri* were captured during sampling operations off the west coast of the Baja California Peninsula (TALUD XV, July-August 2012; TALUD

XVI-B, May-June 2014), in the Gulf of California (a total of nine cruises: TALUD III, September 1991; TALUD IV, August 2000; TALUD V, December 2000; TALUD VI, March 2001; TALUD VII, June 2001; TALUD VIII, April 2005; TALUD IX, November 2005; TALUD X, February 2007), and off the SW coast of Mexico, from Jalisco to Guerrero (TALUD XII, March-April 2009). During these cruises, a total of 228 localities were sampled, from 377 to 2394 m depth. Positional coordinates for each sampling station were obtained using a GPS navigation system. Depth was measured with an EdoWestern analogic recorder (TALUD III-VIII) or a digital recorder (TALUD IX-XVI-B). All the specimens were captured with benthic gear, including an Agassiz dredge (2.5 m width, 1 m high) and a standard benthic sledge (2.35 m width, 0.9 m high), both equipped with a modified shrimp net (ca 5.5 cm stretched mesh size) with a ca 2.0 cm (3/4”) internal lining net. The material collected during this survey is deposited in the Regional Collection of Marine Invertebrates (EMU), at UNAM in Mazatlán, Mexico. The size (carapace length, CL) of all the specimens was measured to the nearest 0.1 mm and size distributions of *B. tanneri* were explored by sex for the entire population sample in the Mexican Pacific. Sexual differences in CL were tested using a Mann-Whitney *U* test (Mann and Whitney 1947). Abbreviations are: St., sampling station; CL, carapace length; M, male; F, female; AD, Agassiz dredge; BS, benthic sledge.

Results

Benthesicymidae Wood-Mason, 1891

Benthesicymus tanneri Faxon, 1893

Figures 2–6

Material examined. Specimens of *B. tanneri* were collected in 44 of the 228 stations visited during the survey (Figure 1).

TALUD III. Material reported by Hendrickx (2001). Additional material. St. 14A (24°38'48"N; 108°26'54"W), Aug 19, 1991, 1M (CL 32.5 mm), AD, 1016–1020 (EMU-4418); St. 14B (24°39'12"N; 108°37'48"W), Aug. 19, 1991, 1F (CL 31.9 mm), AD, 1188–1208 m (EMU-2609); St. 17 (24°33'0"N; 108°50'54"W), Aug 19, 1991, 1M (CL 22.1 mm), AD, 770 m (EMU-4417); St. 24A (25°45'12"N; 109°46'48"W), Aug 24, 1991, 2M (CL 29.0–30.8 mm), AD, 1027–1060 m (EMU-100).

TALUD IV. Material reported by Hendrickx (2001).

TALUD V, St. 5 (22°0'57"N; 106°40'0"W), Dec 13, 2000, 1F (CL 36.3 mm), BS, 1515–1620 m (EMU-5540-A); St. 6 (22°N; 106°48'5"W), Dec 13, 2000, 1F (CL 41.1 mm), BS, 1950–2010 m (EMU-5540-B); St. 19 (23°17'30"N; 107°29'51"W), Dec 15, 2000, 1M (CL 31.1 mm), 3F (CL 29.1–36 mm), BS, 1180–1200 m (EMU-5523-A); St. 26 (24°15'18"N; 108°24'6"W), Dec 16, 2000, 2M (CL 29–30.7 mm), 2F (CL 32–34.2 mm), BS, 1280–1310 m (EMU-5523-B).

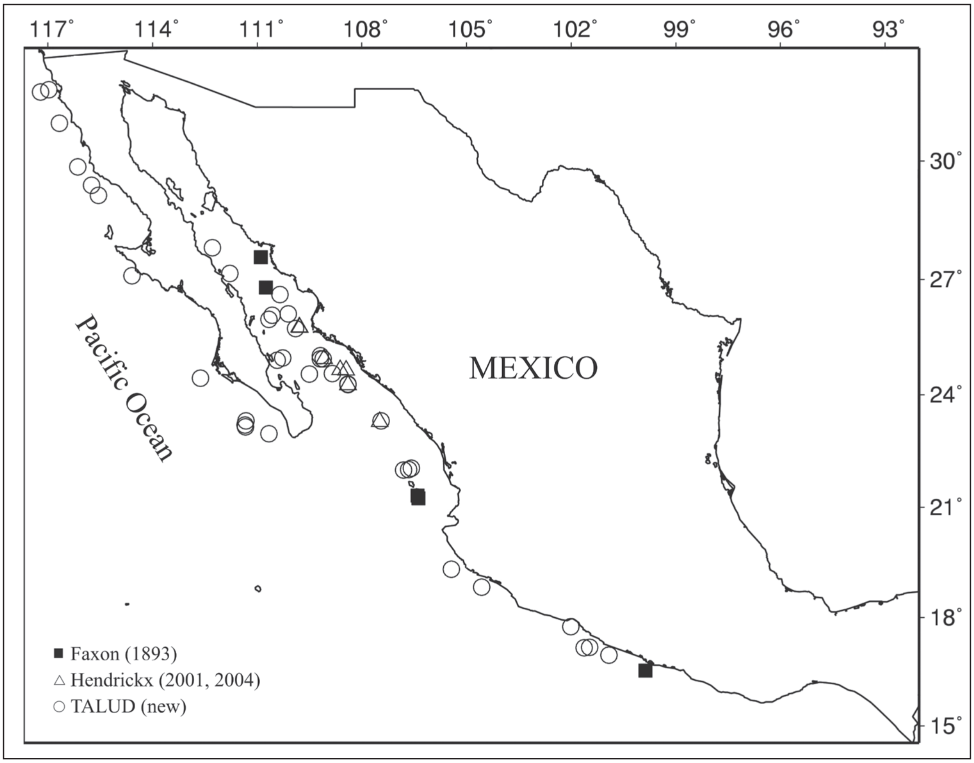

Figure 1. Localities in the Mexican Pacific where *Benthesicymus tanneri* Faxon, 1893 has been collected, including the TALUD project sampling stations and the localities corresponding to the type material collected during the "Albatross" cruises and used by Faxon (1893).

TALUD VI, St. 12 (23°18'36"N; 107°26'56"W), Mar 14, 2001, 1M (CL 32.5 mm), 1F (CL 34.8 mm), BS, 1050–1160 m (EMU-5539-A); St. 19 (24°16'24"N; 108°24'18"W), Mar 15, 2001, 1F (CL 50.4 mm), BS, 1160–1200 m (EMU-5539-B); St. 26 (24°56'18"N; 109°6'42"W), Mar 16, 2001, 1M (CL 33.4 mm), 1F (CL 25.2 mm), BS, 1190–1270 m (EMU-5997-A); St. 27 (25°1'12"N; 109°11'36"W), Mar 16, 2001, 1F (CL 32.3 mm), BS, 1580–1600 m (EMU-5539-C); St. 34 (25°43'50"N; 109°53'59"W), Mar 17, 2001, 1M (CL 31.9 mm), 2F (CL 3025–33.6 mm), BS, 1240–1270 m (EMU-5997-B), and 7M (CL 31.4–34.8 mm), 12F (CL 30.5–42.5 mm), and 3 unsexed specimens (14.5–21.4 mm).

TALUD VII, St. 4 (22°3'18"N; 106°34'42"W), Jun 5, 2001, 1F (CL 37.8 mm), BS, 1190 m (EMU-5541); St. 19 (24°16'12"N; 108°23'42"W), Jun 7, 2001, 1M (CL 11.2 mm) and 1F (CL 34.7 mm), BS, 1160–1180 m (EMU-6004-A); St. 33B (26°6'30"N; 110°6'42"W), Jun 9, 2001, 1F (CL 23.0 mm), BS, 1260–1300 m (EMU-6004-B).

TALUD VIII, St. 10 (24°58'12"N; 110°16'6"W), Apr 17, 2005, 1M (CL 30.4 mm), and 1F (CL 11.2 mm), BS, 1500 m (EMU-8143); St. 3 (24°32'36"N; 109°30'30"W), Apr 16, 2005, 2M (CL 31.9–34.7 mm), 3F (CL 29.2–35.7 mm), BS, 1100 m (EMU-8147).

TALUD IX, St. 20B (25°58'7"N; 110°40'4"W), Nov 14, 2005, 2F (CL 33.7–36.2 mm), BS, 1229–1343 m (EMU-8236).

TALUD X, St. 10 (27°50'5"N; 112°10'7"W), Feb 10, 2007, 1F (CL 32.3 mm), BS, 1399–1422 m (EMU-8030); St. 18 (27°9'6"N; 111°46'54"W), Feb 12, 2007, 1F (CL 31.3 mm), BS, 1526 m (EMU-8118); St. 30 (26°36'50"N; 110°21'10"W), Feb 15, 2007, 1M (CL 29.9 mm), BS, 1203–1213 m (EMU-8203).

TALUD XII, St. 5 (16°58'28"N; 100°55'20"W), Mar 28, 2008, 1F (CL 53.3 mm), BS, 1925–1977 m (EMU-8872); St. 9 (17°10'15"N; 101°37'23"W), Mar 28, 2008, 6F (CL 30.1–35.3 mm), BS, 1392–1420 m (EMU-8874); St. 10 (17°11'18"N; 101°28'30"W), Mar 29, 2008, 3F (CL 21.1–38.7 mm), BS, 1180–1299 m (EMU-10500); St. 13 (17°45'16"N; 102°0'29"W), Mar 30, 2008, 1F (CL 30 mm), BS, 1198 m (EMU-8904); St. 28 (18°50'19"N; 104°34'14"W), Apr 2, 2008, 1F (CL, 38.1 mm), BS, 1101–1106 m (EMU-10499); St. 29 (19°19'37"N; 105°26'20"W), Apr 2, 2008, 1F (CL 44.7 mm), BS, 1609–1643 m (EMU-8873).

TALUD XV, St. 1 (23°18'40"N; 111°19'37"W), Aug 4, 2012, 1F (CL 40.2 mm), BS, 750–850 m (EMU-10435); same station, 5M (CL 17.9–29.1 mm) and 7F (CL 25.3–41.1 mm), BS, 750–850 m (EMU-10434); St. 2 (23°12'2"N; 111°20'50"W), Aug 4, 2012, 4M (CL 32–33.9 mm), 5F (CL 23.2–40.6 mm) and 1Juv. (CL 12.4 mm), BS, 1118–1150 m (EMU-10436); St. 3 (23°9'N; 111°20'W), Aug 4, 2012, 1F (CL 36.4 mm), BS, 1395–1465 m (EMU-10433); St. 5C (23°16'42"N; 110°54'55"W), Aug 5, 2012, 8M (CL 20.5–35.5 mm), BS, 980–1036 m (EMU-10496-A); same station 25F (CL 20.3–40.5 mm), 1M (CL 13.4 mm), BS, 980–1036 m (EMU-10496-B); St. 5F (22°58'15"N; 110°40'17"W), Aug 5, 2012, 1F (CL 39.3 mm), BS, 1035–1108 m (EMU-10432); St. 8 (24°25'48"N; 112°38'6"W), Jul 30, 2012, 1M (CL 29.8 mm), 3F (CL 23.2–41.1 mm), BS, 1212–1235 m (EMU-10431); St. 24 (27°5'42"N; 114°35'30"W), Aug 1, 2012, 2F (CL 25–32.6 mm), BS, 772–786 m (EMU-10430).

TALUD XVI-B, St. 3 (28°42'36"N; 115°50'42"W), May 23, 2014, 2F (CL 30.1–31.0 mm), BS, 1350–1365 m (EMU-10623) St. 6 (29°08'9"N; 115°33'25"W), May 24, 2014, 10M (CL 16.4–29.9 mm) and 9F (CL 16.7–29.5 mm), BS, 1004–1102 m (EMU-10498); St. 8 (29°23'28"N; 115°45'W), May 31, 2014, 1M (CL 35.4 mm), 1F (CL 27 mm), BS, 1416–1480 m (EMU-10438); St. 16 (29°51'N; 116°9'W), May 29, 2014, 4F (CL 23.2–37.2 mm), BS, 1425–1360 m (EMU-10441); St. 23 (30°56'N; 116°40'33"W), May 27, 2014, 1M (CL 33.3 mm), 2F (CL 30.1–32.7 mm), BS, 1296–1340 m (EMU-10439); St. 26 (31°46'3"N; 116°58'12"W), May 26, 2014, 1F (CL 31.4 mm), BS, 982–989 m (EMU-10437); St. 27 (31°42'21"N; 117°13'W), May 27, 2014, BS, 1394–1397 m, 1F (CL 34.7 mm) (EMU-10440) and 1 F (CL 30.5 mm) (EMU-10497).

Size and sex. With 187 specimens available (61 males, CL 11.2–35.5 mm; 122 females, CL 16.7–53.3 mm; 3 unsexed; and 1 juvenile, CL 12.4) (M:F = 1:2), the collection of *B. tanneri* from off western Mexico came from 44 stations and is the largest available to date for this species (Figure 1). The largest specimens measured 103 mm (male; TALUD XV, St. 5C) and 116 mm (female; TALUD XII, St. 5) total length, the latter constituting the largest specimen collected to date. The size of individuals dif-

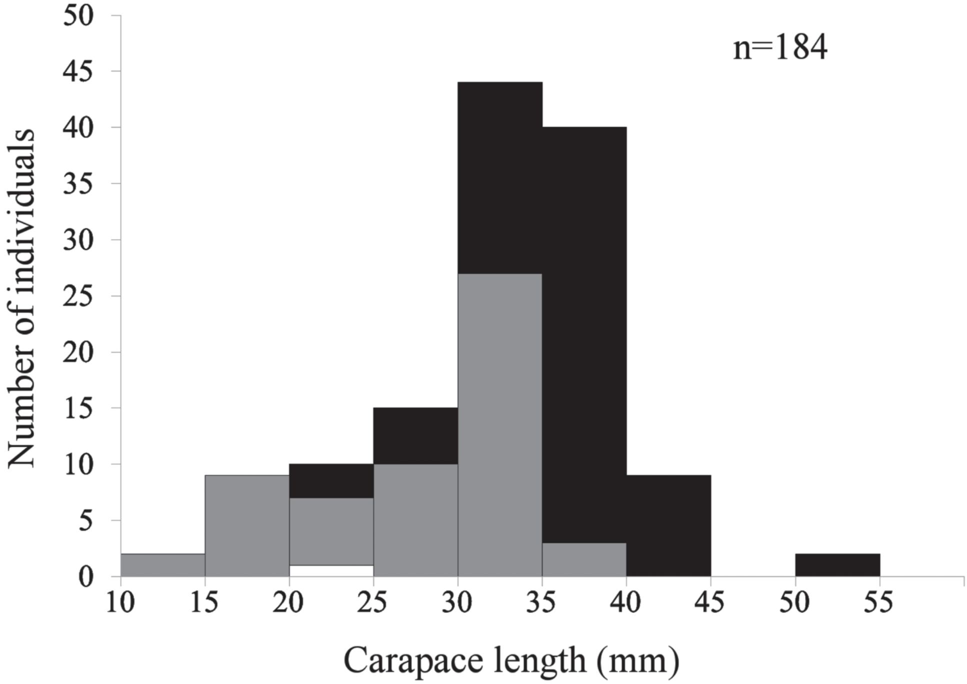

Figure 2. Carapace length distribution of *Benthesicymus tanneri* Faxon, 1893, by sex. White, juveniles; grey, males; black, females.

fered across sexes (Mann-Whitney *U* test, *U*=2058.00, $p<0.001$) with females growing larger than males (Figure 2).

Geographic and bathymetric distributions. The syntype series, collected by the "Albatross", contained 56 males and 78 females (134 specimens) from 22 lots captured over a wide latitudinal range (1°3'S to 27°34'N), and included material from 4 stations in Mexico: off Acapulco and Islas Tres Marías, and in the vicinity of Guaymas (Figure 1). We are not aware of further material collected off western Mexico.

According to Wicksten (1989), Retamal and Jara (2002) and Wicksten and Hendrickx (2003), *B. tanneri* is known from San Diego, California, USA, to Chile. The material currently examined slightly increases the distributional range of *B. tanneri* within the Gulf of California to the north, and indicates that *B. tanneri* occurs all along the west coast of the Baja California Peninsula where it had not been reported previously (Figure 1). In the Mexican Pacific it is a widely distributed and frequently captured species.

The material examined herein was collected between 750 and 2010 m depth with bottom sampling gear. One specimen (TALUD III, St. 17) was collected with a midwater trawl hauled from surface to 770 m depth, in a locality where total depth was 1560 m. All species of *Benthesicymus* occur in deep water and the general depth range for *B. tanneri* is 606–2422 m (Table 1) (Wicksten 1989).

Table 1. Currently known distribution, depth range and maximum size for the species of *Benthesicymus* worldwide. Species list updated according to Fransen and De Grave (2014). MW, midwater trawl; BT, benthic trawl; IK, Isaac Kid midwater trawl; AT, Agassiz (benthic) trawl.

Species	Distribution	Depth range	Size	Source
Benthesicymus altus Spence Bate, 1881	Eastern, central and western Pacific; Atlantic and Indian Oceans	485 m (MW); 916–4089 m; 4130 m (BT)	CL 23.5 mm; TL 120 mm	Spence Bate 1881; Wicksten 1989; Kikuchi and Nemoto 1991, Guzman and Wicksten 2000; Wicksten and Hendrickx 2003
Benthesicymus armatus MacGilchrist, 1905	Arabian Sea	2753 m	TL 157 mm	MacGilchrist 1905
Benthesicymus bartletti S. I. Smith, 1882	Atlantic, eastern Indian and western Pacific Oceans	600–5777 m	CL 34.2 mm; TL 115 mm	Crosnier 1978; D'incao 1998; Tiefenbacher 2001
Benthesicymus brasiliensis Spence Bate, 1881	Atlantic, southern Pacific	600–4720 m	TL 152 mm	Spence Bate 1881; Tiefenbacher 2001
Benthesicymus cereus Burkenroad, 1936	Atlantic	1645–1727 m	CL 25 mm; TL 76 mm	Burkenroad 1936
Benthesicymus crenatus Spence Bate, 1881 (type species)	Northwestern and central Pacific	3530 m (BT); 3530–6350 m; 5469–9726 m	TL 200 mm	Spence Bate 1881; Komai and Komatsu 2009; Jamieson et al. 2009
Benthesicymus howensis Dall, 2001	Western Pacific	1325 m	CL 24.0 mm	Dall 2001
Benthesicymus investigatoris Alcock & Anderson, 1899	Indo-West Pacific; SW Pacific	0–1300 (IK); 1213 (AT); 580–1690 m	CL 27.5 mm; TL 89.5 mm	Kensley 1977; Kikuchi and Nemoto 1991; Dall 2001; Retamal and Moyano 2010
Benthesicymus iridescens Spence Bate, 1881	Atlantic Ocean	3890–6500 m	TL 150 mm; CL 47 mm	Spence Bate 1881; Crosnier 1985; Tiefenbacher 2001
Benthesicymus laciniatus Rathbun, 1906	Eastern Pacific	1471–3393 m	CL 42.6 mm	Wicksten 2004
Benthesicymus seymouri Tirmizi, 1960	Indian Ocean	1789–3716 m	CL 40–59 mm	Crosnier 1985; Pérez-Farfante and Kensley 1997
Benthesicymus strabus Burkenroad, 1936	Pacific Ocean	3530 m (BT)	CL 39.5 mm	Kikuchi and Nemoto 1991
Benthesicymus tanneri Faxon, 1893	Eastern Pacific	606–2422 m	TL 121 mm	Wicksten 1989; Wicksten and Hendrickx 2003; Hendrickx 2004
Benthesicymus tirmiziae Crosnier, 1978	Indian Ocean	1920–2249 m	33 mm CL, 100 mm TL	Crosnier 1978; Peréz-Farfante and Kensley 1997
Benthesicymus urinator Burkenroad, 1936	Indo-Pacific	1789–3716 m; 2500–4200 m; 4120 m (BT)	CL 25.0 mm	Crosnier 1985; Kikuchi and Nemoto 1991, Dall 2001

Of the 15 recognized species of *Benthesicymus* (Table 1), currently known distributions indicate that three are widespread (*B. altus*, *B. bartletti*, *B. investigatoris*), one occurs in both the Atlantic and part of the Pacific (*B. brasiliensis*), one is distributed in the Indo-Pacific (*B. urinator*), three are restricted to the Indian Ocean (or part of it) (*B. armatus*, *B. seymouri*, *B. tirmiziae*), five occur in the Pacific Ocean (*B. crenatus*, *B. howensis*, *B. strabus*, *B. laciniatus*, *B. tanneri*; the latter two only known from the eastern Pacific), and two are restricted to the Atlantic Ocean (*B. iridescens*, *B. cereus*).

On the presence of the hepatic spine in *B. tanneri*. In their identification key of Group II, Kikuchi and Nemoto (1991) indicated that *B. tanneri* possesses a hepatic spine, a character that separates this species from the other four species of their Group II. Guzmán and Wicksten (2000) emphasize that the presence of a hepatic spine was not mentioned in some of the previous literature referring to *B. tanneri* (i.e., Méndez 1981, Wicksten and Hendrickx 1992, Retamal and Soto 1993). Incidentally, the figure provided by Méndez (1981: fig. 62) does not show the presence of an hepatic spine but its reproduction in Hendrickx (1995) does (p. 437), which is an error due to the illustration process in the editorial office. In his preliminary description of *B. tanneri*, Faxon (1893) indicated that "*B. moratus*, Smith [S.-I. Smith, 1886, now recognized as a junior synonym of *B. brasiliensis* Spence Bate, 1881], another allied species [of *B. tanneri*], differs in having a distinct hepatic spine", from which it could be concluded that the type material of *B. tanneri* examined by Faxon (1893) lacks this spine. Re-description by Faxon (1895: 205) repeats essentially the same statement as in 1893, and his lateral illustration of the carapace (Plate H 1a) does not indicate the presence of a hepatic spine, although the lower extension of the cervical carina could easily be confused with a strong spine. Besides, this drawing does not include the presence of the pterygostomial spine either, which is definitively present in *B. tanneri* (see Burkenroad 1936: 52). Revision by Dr. Rafael Lemaitre of part of the material used by Faxon (1893, 1895) in his syntypic series and deposited at the National Museum of Natural History, Washington, DC (USNM 21214; syntypes from the Gulf of California, Mexico) confirms the fact that there is no trace of a hepatic spine on the specimens examined. Another revision by Adam Baldinger of one of the syntypes of *B. tanneri* (MCZ-4662) deposited at the Museum of Comparative Zoology at Harvard also clearly indicates the absence of a hepatic spine (Figure 3A). An illustration of a large specimen of *B. tanneri* collected during this survey is also provided for comparison (Figure 3B). References to this spine in earlier literature (Kikuchi and Nemoto 1991, Hendrickx 1995, Dall 2001) are therefore in error. Consequently, the groups definition presented by Kikuchi and Nemoto (1991) have to be altered because all species of Group II as defined by these authors in their key lack the hepatic spine which is otherwise present in seven of the ten species of their Group I. Moreover, the identification key proposed by Dall (2001) should be partly modified.

Reproductive organs. While studying fine morphology of *B. carinatus* (now included in *Altelatipes*), Tavares (2009) noted the lack of basic information related with the description and development of the reproductive organs of *Benthesicymus* s.l. The male petasma of *B. tanneri* was illustrated by Faxon (1895) and by Hendrickx and

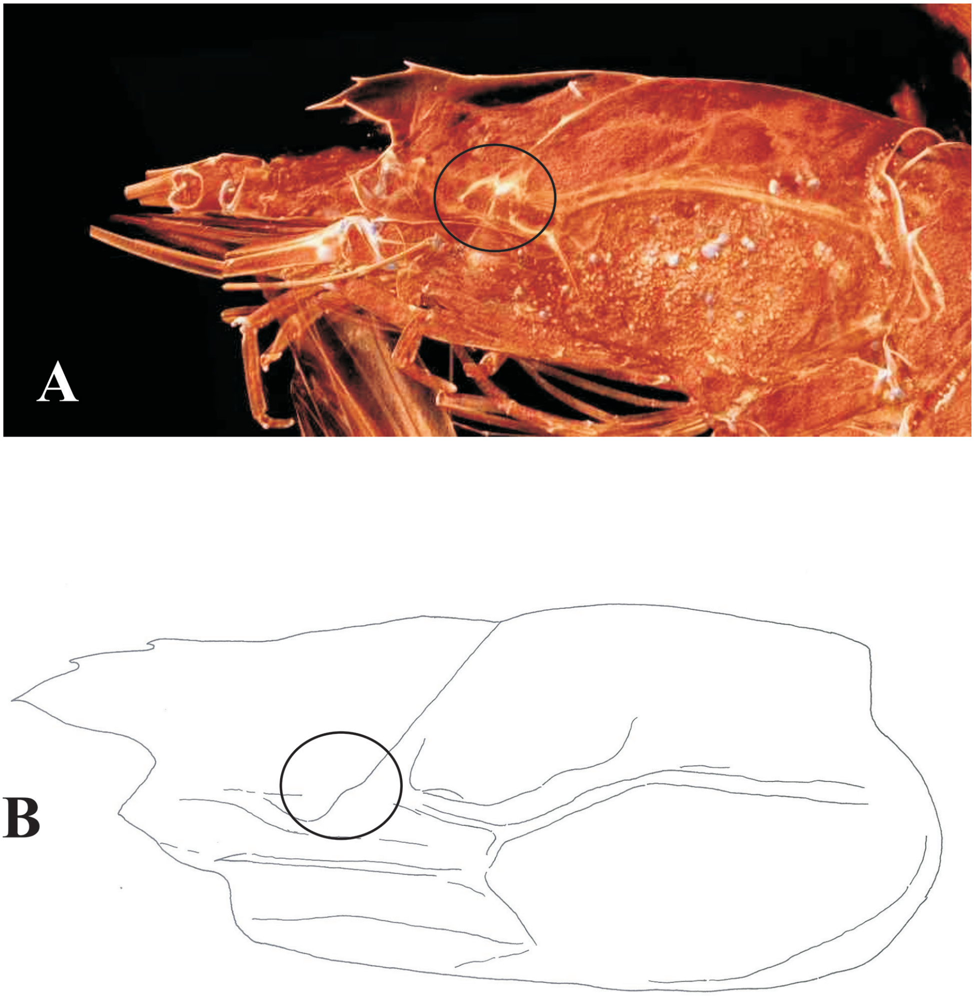

Figure 3. *Benthesicymus tanneri* Faxon, 1893. **A** Lateral view of syntypic specimen (MCZ-4662) **B** Lateral view of female (CL 40.6 mm) (EMU-10436). Circles indicate area where a hepatic spine is observed in some species of the genus.

Estrada-Navarrete (1996). Material examined collected in station 6 of the TALUD XVI-B cruise includes small and medium-size males with immature petasma (Figure 4A–D). The smallest male with visible petasma was 11.2 mm CL, in which a small bud without any elaborated structure could be seen. A slightly larger male (CL 16.4 mm) had a similar petasma (Figure 4D). However, another young male from station 19 of TALUD VII cruise with CL 11.2 mm (i.e., smaller than the male of Figure 4D) presented a relatively larger petasma (Figure 4E). The crescent-shape lateral process, which is typical of *B. tanneri*, is not yet developed in males of CL 17.5 mm (Figure 4C). In a male of CL 29.9 mm the two sections (left and right) of the petasma are well developed (Figure 4B) but not yet united medially.

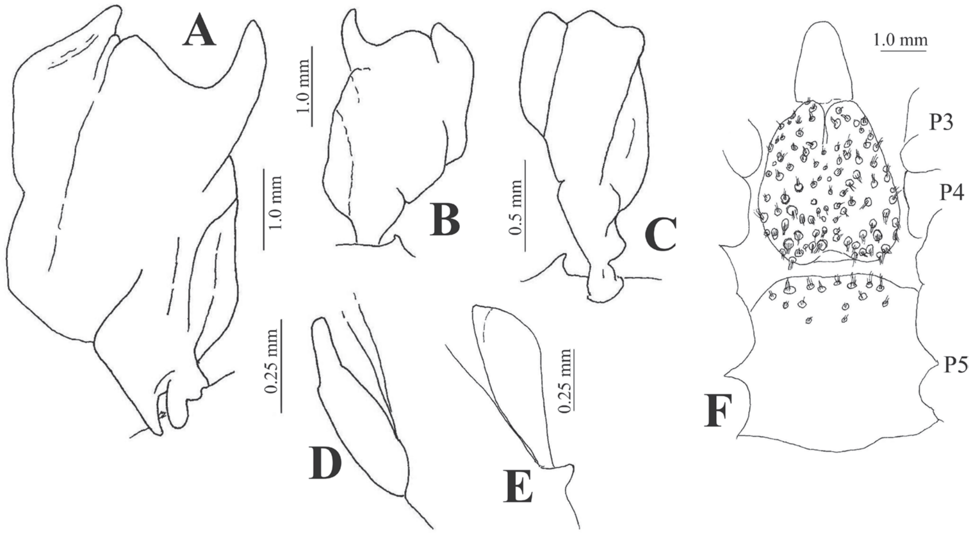

Figure 4. *Benthesicymus tanneri* Faxon, 1893. Anterior view of petasma (**A–E**) of males of different carapace length (**A–D** EMU-10498; **E** EMU-6004-A) and thelycum (**F**) of a mature female (EMU-10441). **A** CL 29.9 mm; **B** CL 22.3 mm; **C** CL 17.5 mm; **D** CL 16.4 mm; **E** CL 11.2 mm; **F** CL 36.6 mm.

The fully developed petasma (Figure 5A–D) of *B. tanneri* (CL ≥ 35 mm) is clearly distinct from known petasma of mature males of nine species of the genus in the presence of the lateral crescent-shape process. In *B. altus*, *B. brasiliensis*, *B. crenatus* (the type species of the genus), *B. investigatoris* Alcok & Anderson, 1899, *B. iridescens* Spence Bate, 1881, *B. laciniatus*, *B. seymouri* Tirmizi, 1960, *B. strabus* Burkenroad, 1936, and *B. urinator* Burkenroad, 1936, the petasma lacks the lateral crescent-shape process (see A. Milne Edwards and Bouvier 1909, Burkenroad 1936, Crosnier 1978, 1985, Hendrickx 1996, Kikuchi and Nemoto 1991) (see below for the case of *B. bartletti* S.I. Smith, 1882). It should be noted that figure 1, page 28, of Burkenroad (1936) is labeled "*Benthesicymus laciniatus* Rathbun", which is most certainly an error, and this illustration likely belongs to *B. crenatus*, as indicated earlier in the text by the author. Burkenroad (1936: fig. 35) also provided an illustration of the petasma of *B. cereus* Burkenroad, 1936, probably a juvenile. This figure lacks a lateral crescent-shape process but, as in the case of *B. tanneri* (see Figures 3, 4), this process may appear later during the growth of the species. Of the remaining three species of *Benthesicymus*, a crescent-like process has been described only in *B. tirmiziae* Crosnier, 1978 (but see below). The petasma of *B. howensis* Dall, 2001, remains undescribed as the species (originally described as a new subspecies of *B. urinator*) is known only from the two females of the type material. We were not able to locate an illustration of the petasma of *B. armatus* MacGilchrist, 1905. Another question remains open as far as illustrations of petasma in literature are concerned. Peréz-Farfante and Kensley (1997: fig. 27) provided an illustration of both the petasma and the thelycum of a species which certainly belongs to *Benthesicymus*; however, the figure caption is the same as the one inserted in figure

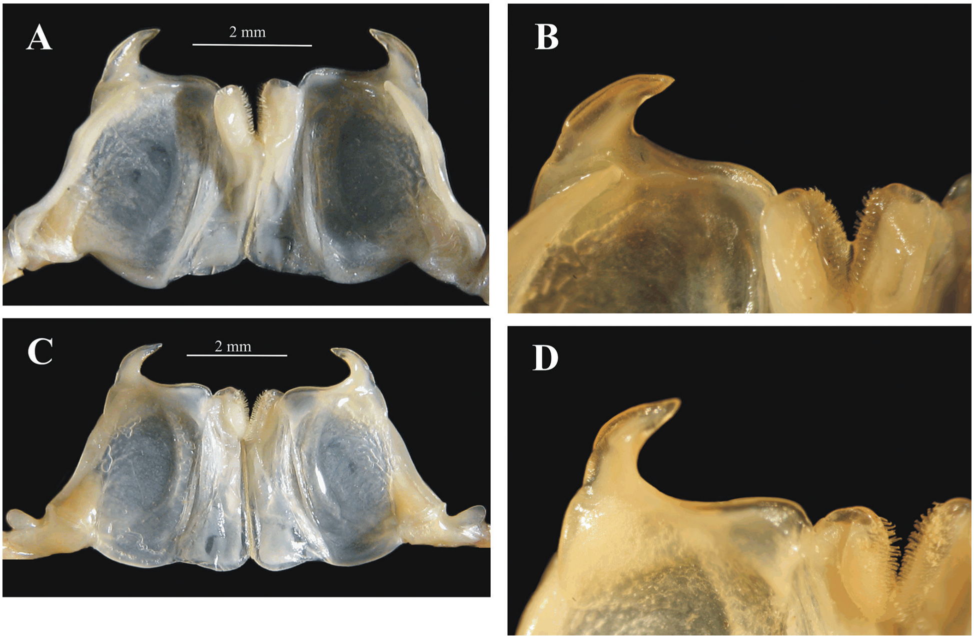

Figure 5. *Benthesicymus tanneri* Faxon, 1893. Petasma of a fully mature male (CL 35.7 mm) (EMU-8147) **A** Posterior view **B** Same, detail of ventral margin **C** Anterior view **D** Same, detail of ventral margin.

25 of the same monograph (i.e. for *Bentheogennema intermedia* (Spence Bate, 1888)) and it was therefore difficult to assess to which species of the genus this figure actually belongs to. A search by Rose Gulledge, Museum specialist at the US National History Museum, Smithsonian Institution crustacean department, Maryland, USA, was successful in finding the original plates prepared by the illustrator of Peréz-Farfante and Kensley (1997). Pencil markings and notes on the plates indicate that the petasma and thelycum of figure 27 belong to *Benthesicymus bartletti*, and that "species in book is wrong [...] must say *Benthesicymus bartletti*". Consequently, *B. bartletti* represents a third species featuring a crescent-shaped lateral process on the petasma, as *B. tanneri* and *B. tirmiziae* do.

The female thelycum of *B. tanneri* was roughly illustrated by Faxon (1895, plate H-1b) and is illustrated herein (Figure 4F). A small tuft of setae is clearly observed arising from each minute pit of the thelycum middle plate (sternite XIII). Of the two groups of species considered by Burkenroad (1936) in his synopsis of *Benthesicymus*, Group I possesses a "thelycum without well-defined receptacles between the twelfth and the thirteenth sternites, the scutes of the twelfth and thirteenth sternites being simple and unexpanded". Group II posseses "well-defined cavities between the twelfth and the thirteenth sternites, the scutes of the thirteenth sternites being broadly expanded to overlap the sternal surface proper". Based on these criteria *B. tanneri* belongs to Group II, with the scutes of sternite XIII broadly expanded (Figure 4F).

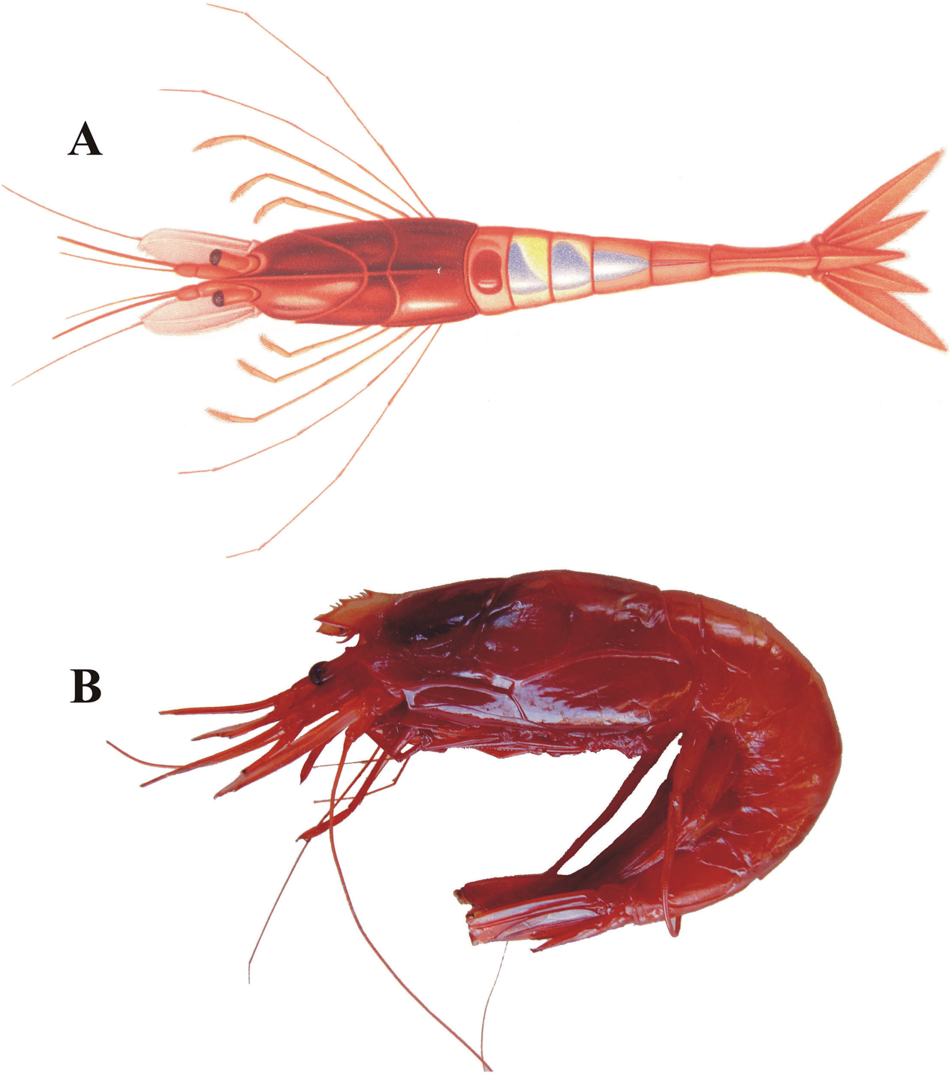

Figure 6. *Benthesicymus tanneri* Faxon, 1893. **A** Dorsal view of one of the syntypes used by Faxon (1893) (from Faxon 1895) **B** Fresh specimen female, CL 30 mm, lateral view (EMU-8904).

Color. The color of fresh specimens was described by Faxon (1895: 207) and a color drawing (Plate H-1) was added to his contribution (reproduced here as Figure 6A). All specimens collected during the TALUD survey presented the typical "deep red" color (Figure 6B) described by Faxon (1895). The large patch of bright blue color on the back of the abdominal somites 2–4 mentioned by Faxon (op. cit.) and also observed by Moscoso (2012) actually corresponds to the gonads of mature specimens that extend backward from the thoracic area (pers. observ.).

Fishery resource. Although it reaches a size (i.e., over 115 mm total length) comparable with other species of Dendrobranchiata used as food, *B. tanneri* is not currently subject to any commercial exploitation. It has been considered a potential fisheries resource for the area (see Hendrickx 1995) to a large extent because it occurs together with other species of established potential for deep-water fisheries (e.g., *Heterocarpus affinis* Faxon, 1893, *Haliporoides diomedeae* Faxon, 1893) (Barriga et al. 2009). Since 2004, the Peru fishery program has included *B. tanneri* in a short list of sub-exploited deep-water shrimps subject to "exploratory fishing" in Peruvian waters (Ministerio de la Producción 2004). In the specific case of the western central Pacific, Chan (1998) reported the presence of six species of *Benthesicymus* in this area, but none was considered of importance to fishery, even as a potential resource, probably because this genus has nowhere been reported to be abundant. The 15 species of *Benthesicymus* known to date are from mid-sized (from ca 70–80 mm TL) to large (ca 200 mm TL) (Table 1) but are all from deep-water, thus rending any exploitation attempt very complex.

Key to the species of *Benthesicymus* from the eastern Pacific

1a	Posterolateral margin of fifth abdominal somite with small spines.... ***B. laciniatus***
1b	Posterolateral margin of fifth abdominal somite without spines **2**
2a	Petasma ventral margin strongly convex, without lateral crescent-shape process. Thelycum sternite XIII plate smooth, without small pits and setae........ .... ***B. investigatoris***
2b	Petasma ventral margin straight to slightly concave, with or without lateral crescent-shape process. Thelycum sternite XIII plate bearing small pits....... **3**
3a	Petasma with strong ventrolateral crescent-shape process. Thelycum sternite XIII plate longer than wide, shallow anterior notch .... ***B. tanneri***
3b	Petasma without ventrolateral crescent-shape process. Thelycum sternite XIII plate wider than long, deep anterior notch.. ***B. altus***

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neri deposited in the USNM and providing useful information on its morphology, and Adam Baldinger, Museum of Comparative Zoology at Harvard, Massachussets, USA, for providing the photograph in Figure 3A. We thank Raymond Bauer for contacting Rose Gulledge, National Museum of Natural History, Maryland, USA, who kindly provided scanned images of the original material used in figure 27 of Pérez-Farfante and Kensley (1997) monograph. Mercedes Cordero Ruiz is acknowledged for preparing Figure 3, and editing Figures 1–2 and the final version of the manuscript. We also thank Ana K. Barragán (SNI III assistant, CONACyT) for her help with laboratory work during this study and José Salgado B. for photograph of Figure 6 B. Work by Vanesa Papiol was supported by a DGAPA, Universidad Nacional Autónoma de México, postdoctoral grant.

References

Barriga E, Salazar C, Palacios J, Romero M, Rodríguez A (2009) Distribución, abundancia y estructura poblacional del langostino rojo de profundidad *Haliporoides diomedeae* (Crustacea: Decapoda: Solenoceridae) frente a la zona norte de Perú (2007–2008). Latin America Journal of Aquatic Research 37(3): 371–380.

Burkenroad M (1936) The Aristaeinae, Solenocerinae and pelagic Penaeinae of the Bingham Oceanographic Collection. Bulletin of the Bingham Oceanographic Collection 5(2): 1–151.

Chan T-Y (1998) Shrimps and prawns In: Carpenter KE, Niem VH (Eds) The living marine resources of the western central Pacific. Vol. 2. Cephalopods, crustaceans, holothurians and sharks. FAO, Roma, 852–971.

Cornejo-Antepara M (2010) Los crustáceos decápodos de aguas profundas del mar ecuatoriano. Master Thesis, Universidad de Guayaquil, Facultad de Ciencias Naturales, Guayaquil, Ecuador.

Crosnier A (1978) Crustacés décapodes Pénéides Aristeidae (Benthesicyminae, Aristeinae, Solenocerinae). Faune de Madagascar. ORSTOM, CNRS (Paris) 46: 1–197.

Crosnier A (1985) Crevettes pénéides d'eaux profondes récoltées dans l'océan Indien lors des campagnes BENTHEDI, SAFARI I et II, MD 32/REUNION. Bulletin du Muséum National d' Histoire Naturelle, Paris (4) 7, section A, 4: 839–877.

Dall W (2001) Australian species of Aristeidae and Benthesicymidae (Penaeoidea: Decapoda). Memoirs of the Queensland Museum 46(2): 409–441.

De Grave S, Fransen CHJM (2011) Carideorum catalogus: the recent species of the dendrobranchiate, stenopodidean, procarididean and caridean shrimps. Zoologische Mededelingen, Leiden 85: 195–588.

D'Incao F (1998) The Brazilian species of the family Aristeidae Wood-Mason (Crustacea: Decapoda). Journal of Natural History 32: 1509–1518. doi: 10.1080/00222939800771041

Faxon W (1893) Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross", during 1891, lieut. Commander Z.L. Tanner, U.S.N., commanding. VI. Preliminary descriptions of new species of Crustacea. Bulletin of the Museum of Comparative Zoology at Harvard University 24 (7): 149–220.

Faxon W (1895) Reports on an exploration off the west coast of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross", during 1891, lieut. Commander Z.L. Tanner, U.S.N., commanding. XV. The stalk-eyed Crustacea. Memoirs of the Museum of Comparative Zoology at Harvard College 18: 1–292.

Fransen C, De Grave S (2014) *Benthesicymus* Spence Bate, 1881. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=106811 [2014–12–09]

Guzman G, Wicksten MK (2000) The subfamily Benthesicyminae Bouvier, 1908 (Decapoda, Dendrobranchiata) in northern Chile (18° to 22°S). Crustaceana 73(8): 925–931. doi: 10.1163/156854000504985

Hendrickx ME (1993) Crustáceos Decápodos del Pacífico Mexicano. In: Salazar-Vallejo SI, González EN (Eds) Biodiversidad Marina y Costera de México. Comisión Nacional de Biodiversidad and CIQRO, Mexico, DF, 271–318.

Hendrickx ME (1995) Camarones. In: Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem VH (Eds) Guía FAO para la identificación de especies para los fines de la pesca. Pacífico centro-oriental. Vol. I. Plantas e Invertebrados. FAO, Roma, 417–537.

Hendrickx ME (1996) Los camarones Penaeoidea bentónicos (Crustacea: Decapoda: Dendrobranchiata) del Pacífico mexicano. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad e Instituto de Ciencias del Mar y Limnología, UNAM, México, DF, 148 pp.

Hendrickx ME (2001) Occurrence of a continental slope decapod crustacean community along the edge of the minimum oxygen zone in the southeastern Gulf of California, Mexico. Belgian Journal of Zoology 131 (Suppl. 2): 95–109.

Hendrickx ME (2004) Distribution and estimation of body size and weight of four species of deep water shrimps in the SE Gulf of California, Mexico. Crustaceana 76 (9): 1025–1036.

Hendrickx ME, Estrada-Navarrete FD (1996) Los camarones Pelágicos (Crustacea: Dendrobranchiata y Caridea) del Pacífico mexicano. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad e Inst. Cienc. Mar y Limnol., UNAM, México, DF, 157 pp.

Jamieson AJ, Fujii T, Solan M, Matsumoto AK, Bagley PM, Priede IG (2009) First findings of decapod crustacea in the hadal zone. Deep-Sea Research I 56: 641–647. doi: 10.1016/j.dsr.2008.11.003

Kameya A, Castillo R, Escudero L, Tello E, Blaskovic V, Córdova J, Hooker Y, Gutiérrez M, Mayor S (1997) Localización, distribución y concentración de langostinos rojos de profundidad Crucero BIC Humboldt 9607–08. 18 de julio a 06 de agosto de 1996. Publicación Especial, Instituto del Mar de Perú, 47 pp.

Kensley B (1977) The South African Museum's Meiring Naude cruises. Part 5. Crustacea, Decapoda, Reptantia & Natantia. Annals of the South African Museum 74(2): 13–44.

Kikuchi T, Nemoto T (1991) Deep-sea shrimps of the genus *Benthesicymus* (Decapoda: Dendrobranchiata) from the western north Pacific. Journal of Crustacean Biology 11(1): 64–89. doi: 10.2307/1548545

Komai T, Komatsu H (2009) Deep-sea shrimps and lobsters (Crustacea: Decapoda) from Northern Japan collected during the project "Research on Deep-sea fauna and pollutants off Pacific coast of Northern Japan". In: Fujita T (Ed.) Deep-sea Fauna and Pollutants off Pacific coast of Northern Japan. National Museum of Nature and Science Monographs 39: 495–580.

MacGilchrist AC (1905) XXVII. Natural History Notes from the R.I.M.S. 'Investigator,' Capt. T. H. Henning, R. N. (retired), commanding. Series III., No. 6. An Account of the new and some of the rarer Decapod Crustacea obtained during the Surveying Seasons 1901–1904. The Annals and Magazine of Natural History, Series 7, 15(87): 234–268.

Mann HB, Whitney DR (1947) On a test of whether one of two random variables is stochastically larger than the other. Annals of Mathematical Statistics 18(1): 50–60. doi: 10.1214/aoms/1177730491

Méndez M (1981) Claves de identificación y distribución de los langostinos y camarones (Crustacea: Decapoda) del mar y ríos de la costa del Perú. Boletín del Instituto del Mar de Perú 5: 1–170.

Milne-Edwards A, Bouvier EL (1909) Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic coast of the United States (1880), by the U.S. Coast Survey Steamer "Blake", Lieut.-Com. C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. 44. Les Pénéides et Sténopides. Memoirs of the Museum of Comparative Zoology at Harvard College 27(3): 177–274.

Ministerio de la Producción (2004) Resolución Directorial 174–2004-Produce/DNEPP. www2.produce.gob.pe/dispositivos [Consulted in October 2014]

Moscoso V (2012) Catálogo de crustáceos decápodos y estomatópodos del Perú. Boletín del Instituto del Mar del Perú 27 (1–2): 1–208.

Peréz-Farfante I, Kensley B (1997) Penaeoid and sergestoid shrimps and prawns of the world. Keys and diagnoses for the families and genera. Mémoirs du Muséum national d'histoire naturelle 175: 1–233.

Rathbun MJ (1904) Decapod crustaceans of the northwest coast of North America. Harriman Alaska Expedition 10: 1–190.

Retamal M, Soto R (1993) Crustáceos decápodos abisales de la zona Arica, Iquique. Estudios Oceanológicos 12: 1–8.

Retamal MA, Jara C (2002) La Carcinología en Chile. In: Hendrickx ME (Ed.) Contributions to the Study of East Pacific Crustaceans 1 [Contribuciones al Estudio de los Crustáceos del Pacífico Este 1]. Instituto de Ciencias del Mar y Limnología, UNAM, México, DF, 195–208.

Retamal MA, Moyano HI (2010) Zoogeografía de los crustáceos decápodos chilenos marinos y dulceacuícolas. Latin America Journal of Aquatic Research 38(3): 302–328.

Rodríguez de la Cruz MC (1987) Crustáceos Decápodos del Golfo de California. Secretaria de Pesca, México, DF, 305 pp.

Schmitt WL (1921) The marine decapod Crustacea of California with special reference to the decapod Crustacea collected by the United States Bureau of Fisheries Steamer "Albatross" in connection with the biological survey of San Francisco Bay during the years 1912–1913. University of California Publications in Zoology 23: 1–470.

Spence Bate C (1881) On the Penaeidea. Annals and Magazine of Natural History 5(8): 169–196.

Tavares C (2009) New record of *Benthesicymus carinatus* Smith, 1884 (Decapoda: Benthesicymidae), with some notes on its morphology deduced from SEM observations. Cahiers de Biologie Marine 50(2): 199–205.

Tiefenbacher L (2001) Recent samples of mainly rare decapod crustacea taken from the deep-sea floor of the southern west Europe basin. Hydrobiologia 449: 59–70. doi: 10.1023/A:1017524600732

Vargas R, Wehrtman IS (2009) Decapod Crustaceans. Part 16. In: Wehrtmann IS, Cortés J (Eds) Marine Biodiversity of Costa Rica, Central America. Monographiae Biologicae 86, Springer Science, 209–236.

Wicksten MK (1989) Ranges of offshore decapod crustaceans in the eastern Pacific Ocean. Transactions of the San Diego Society of Natural History 21(19): 291–316.

Wicksten MK (2004) The status of *Benthesicymus laciniatus* Rathbun (Decapoda, Penaeoidea, Benthesicymidae) in the Northeastern Pacific. Bulletin of the Southern California Academy of Sciences 103(2): 93–94.

Wicksten MK, Hendrickx ME (1992) Checklist of Penaeoid and Caridean shrimps (Decapoda: Penaeoidea, Caridea) from the eastern tropical Pacific. Proceeding of the San Diego Society of Natural History 9: 1–11.

Wicksten MK, Hendrickx ME (2003) An updated checklist of benthic marine and brackish water shrimps (Decapoda: Penaoidea, Stenopodidea, Caridea) from the Eastern Tropical Pacific. In: Hendrickx ME (Ed.) Contributions to the Study of East Pacific Crustaceans 2. [Contribuciones al Estudio de los Crustáceos del Pacífico Este 2]. Instituto de Ciencias del Mar y Limnología, UNAM, México, DF, 49–76.

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RESEARCH ARTICLE

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Rediscovery and redescription of the sharpshooter *Kogigonalia incarnata* (Germar, 1821), comb. n. (Hemiptera, Cicadellidae, Cicadellini) from the Atlantic Forest of Brazil, with a key to the species of the genus

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Abstract

The Brazilian sharpshooter *Tettigonia incarnata* Germar, 1821 was treated as *incertae sedis* in the most comprehensive and recent monograph of the New World Cicadellini. We have been able to identify male and female specimens of *T. incarnata* from northeastern and southeastern Brazil using high-resolution images of two syntypes deposited in the Museum für Naturkunde, Universität Humboldt, Berlin. Here we transfer *T. incarnata* to the genus *Kogigonalia* Young, 1977 and provide a detailed redescription of this species, including information on intraspecific color variation. In addition, we provide an updated key to the species of *Kogigonalia*. This is the first record of the genus from Brazil. *Kogigonalia incarnata* **comb. n.** can be recognized, among other features, by the subgenital plates with a distinct emargination at outer margin, aedeagus with a ventral unpaired process near midlength of shaft, and female sternite VII bearing an elongate strong projection on posterior margin.

Keywords

Cicadellinae, leafhopper, morphology, Neotropics, taxonomy

Introduction

Six species were included by Young (1977) in the South American sharpshooter genus *Kogigonalia* Young, 1977 (McKamey 2007, Wilson et al. 2009): *K. cajana* Young, 1977 (Peru), *K. dietzi* Young, 1977 (Venezuela; type species), *K. enola* Young, 1977 (French Guiana), *K. resoluta* (Melichar, 1926) (Peru), *K. spectabilis* (Melichar, 1932) (Colombia, Peru), and *K. zarumoidea* Young, 1977 (Colombia). Young (1977: 82) included *Kogigonalia* in his *Dilobopterus* generic group, a diverse assemblage of 27 genera. Within the *Dilobopterus* group, he considered *Kogigonalia* to be closely related to *Poeciloscarta* Stål, 1869, *Cardioscarta* Melichar, 1932, and *Janastana* Young, 1977. *Kogigonalia* can be distinguished from these three genera, as well as from other Cicadellini, by the following combination of features: crown with anterior margin broadly rounded; thorax with pronotal width greater than transocular width of head, lateral margins of pronotum convergent anteriorly; male pygofer well produced posteriorly, without a dorsal lobe; subgenital plates usually not extending posteriorly as far as pygofer apex; styles usually without a lateral lobe; paraphyses, when present, long-stalked and with a pair of narrowly separated divergent rami; female abdominal sternite VII (known only from *K. spectabilis* and *K. resoluta*) with a pair of elongate lateral processes or projections.

Tettigonia incarnata was described by Germar (1821) based on material from Brazil ("habitat in Brasilia"). In his monograph of the New World Cicadellini, Young (1977: 1105) treated *T. incarnata* as *incertae sedis* because he was not able to examine specimens of this species. We have been able to identify male and female specimens of *T. incarnata* from northeastern and southeastern Brazil using high-resolution images of two syntypes (see Wilson et al. 2009) deposited in the Museum für Naturkunde, Universität Humboldt, Berlin. Two additional syntypes reside in the Germar collection in the Ivan Franko National University, Lviv (Shydlovskyy and Holovachov 2005, Holovachov 2008) but were not available for study. The original description of Germar (1821) and the reasonably detailed redescription and color figure of the body provided by Signoret (1853) were also very useful, allowing a precise identification of our specimens. Here we transfer *T. incarnata* to the genus *Kogigonalia* and provide a detailed redescription of this species, including information on intraspecific color variation. In addition, we provide an updated key to the species of the genus. This is the first record of the genus *Kogigonalia* from Brazil.

Material and methods

Techniques for preparation of male and female genital structures follow Oman (1949) and Mejdalani (1998), respectively. Dissected genital parts are stored in small vials with glycerin and attached below the specimens, as suggested by Young and Beirne (1958). The descriptive terminology adopted herein follows mainly Young (1977), except for the facial areas of the head (Hamilton 1981, Mejdalani 1993, 1998) and the female genitalia (Nielson 1965, Hill 1970). Use of the term gonoplac (= third ovipositor valvula) and the names of the sculptured areas of the first ovipositor valvulae follow Mejdalani (1998). Photographs of the first and second valvulae were taken with a digital camera attached to an optical microscope. The specimens studied belong to the following institutions: Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ, Rio de Janeiro); Coleção Entomológica Prof. José Alfredo P. Dutra, Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (DZRJ, Rio de Janeiro); Coleção de Entomologia Pe. Jesus S. Moure, Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná (DZUP, Curitiba); and Museum für Tierkunde (MTD, Dresden).

Results

Genus *Kogigonalia* Young, 1977

Kogigonalia incarnata (Germar, 1821), comb. n.

Figs 1, 2, 3a–c

Remarks. *Tettigonia incarnata* Germar, 1821: 69. Catalogued (as *Amblyscarta incarnata*) by Metcalf (1965), McKamey (2007), and Wilson et al. (2009). Redescribed by Blanchard (1840: 190) and Signoret (1853: 684, pl. 22, fig. 11). Four syntypes (two males, two females) from "Bahia" (northeastern Brazil) are deposited in the Museum für Naturkunde, Universität Humboldt, Berlin; we have studied high-resolution images (Fig. 3a–b, dorsal view of the body) of a male and a female syntype (see Wilson et al. 2009). Two additional syntypes are deposited in the Germar collection in the Ivan Franko National University, Lviv (Shydlovskyy and Holovachov 2005: 41, Holovachov 2008).

Description. Length of male 10.4–11.3 mm (n = 3), female 10.8–11.9 mm (n = 3).

Head (Fig. 1a), in dorsal view, well produced anteriorly, median length of crown approximately 7/10 interocular width and 4/10 transocular width; anterior margin broadly rounded; without carina at transition from crown to face; ocelli located on imaginary line between anterior eye angles, each approximately equidistant between adjacent eye angle and median line of crown; surface without sculpturing or setae; frontogenal sutures extending onto crown and attaining ocelli. Antennal ledges, in dorsal view, not protuberant; in lateral view, with anterior margins oblique and slightly concave. Frons swollen, muscle impressions distinct. Epistomal suture interrupted medially. Clypeus not produced; upper half continuing contour of frons, lower half more nearly horizontal; apex convex.

Thorax (Fig. 1a), in dorsal view, with pronotal width greater than transocular width; pronotum with lateral margins convergent anteriorly; posterior margin rectilinear or slightly concave; disk without sculpturing or setae; dorsopleural carinae declivous anteriorly, incomplete. Mesonotum with scutellum not transversely striate.

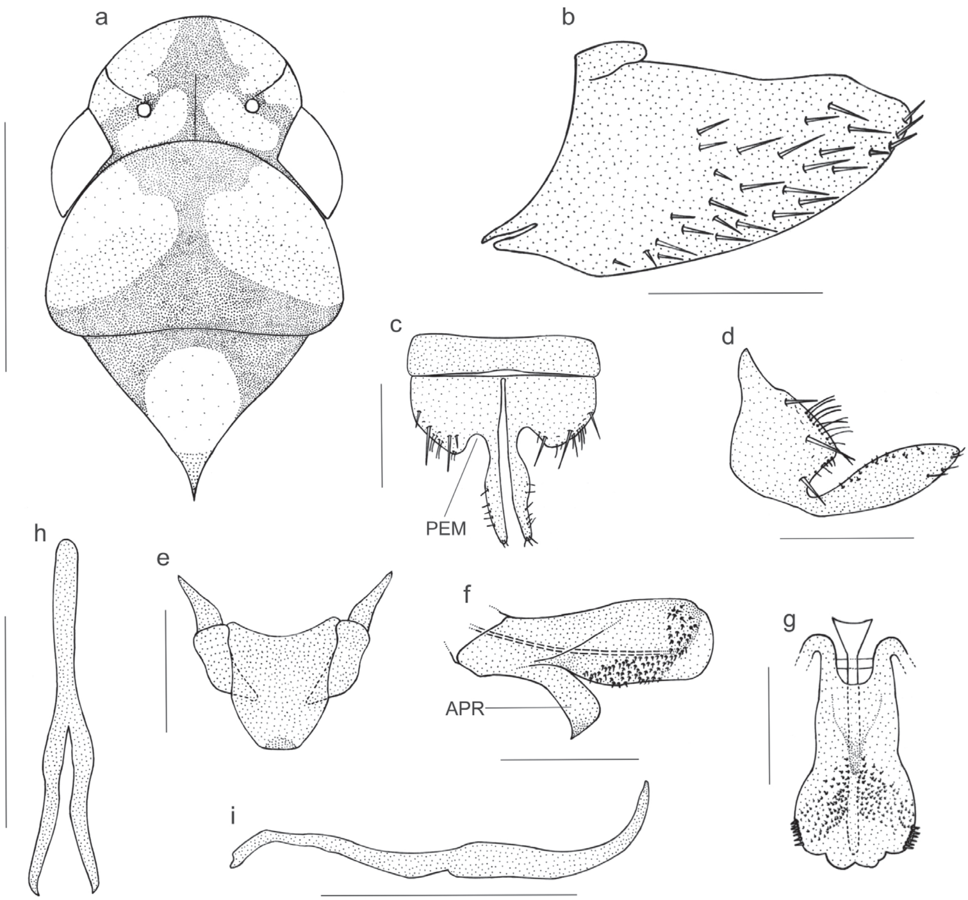

Figure 1. *Kogigonalia incarnata* (Germar, 1821), comb. n. **a** crown, pronotum, and mesonotum, dorsal view. **b–i** male terminalia: **b** pygofer, lateral view **c** valve and subgenital plates, ventral view **d** subgenital plate, lateral view **e** connective and styles, dorsal view **f** aedeagus, lateral view **g** aedeagus, ventral view **h** paraphyses, dorsal view **i** paraphyses, lateral view. APR = aedeagal ventral process; PEM = emargination of subgenital plate. Scale bars: **a** = 2 mm, **b, h, i** = 1 mm, **c–g** = 0.5 mm.

Forewings coriaceous, venation (except on apical third) not very distinct; membrane well delimited, including first and second apical cells and distal portions of third and fourth apical cells; base of fourth apical cell located more proximally than base of third; with three closed anteapical cells, their bases located more proximally than apex of clavus. Hind wings with vein R_{2+3} incomplete. Hind legs with femoral setal formula 2:1:1; length of first tarsomere greater than combined length of second and third; with two parallel rows of small setae on plantar surface.

Color (Fig. 3a–c). Ground color of anterior dorsum (crown, pronotum, and mesonotum) yellow. Crown with dark brown to black median spear-shaped mark (size variable and may bear lateral extensions, sometimes covering much of coronal surface, with only lateroanterior portions remaining yellow); other variable minor dark brown to black marks also present. Pronotum with conspicuous T-shaped dark brown to black mark, formed by median longitudinal stripe and posterior transverse stripe, anterior pronotal margin with transverse dark brown to black mark at base of “T” (pronotal marks varying from strong to faint or incomplete, sometimes covering much of pronotal surface, with only a pair of lateral areas remaining yellow); lateral portions of disk with variable brown or orange areas. Mesonotum with basal portion largely and variably dark brown to black; posterior portion of scutellum reddish-brown. Ground color of forewings reddish-brown; with or without three large orange or yellow areas, the first and largest on corium and clavus at basal third of wing, the second extending from costal area over clavus and forming transcommissural stripe, and the third extending from costal margin to outer margin of first apical cell (orange or yellow areas, when present, varying from distinct to faint); membrane brown. Face, thorax and legs, and venter of abdomen mostly yellow; frons with or without dark brown to black longitudinal stripe (continued from coronal spear-shaped mark); dorsum of abdomen red; male pygofer reddish.

Male genitalia with pygofer (Fig. 1b), in lateral view, strongly produced posteriorly; posterior margin narrowly rounded; without processes; macrosetae distributed mostly on posterior half and extending anteriorly along ventral margin. Valve (Fig. 1c), in ventral view, subrectangular. Subgenital plates (Fig. 1c–d) much shorter than pygofer; in ventral view, with basal half broad and apical half abruptly and strongly narrowed; transition from broad to narrow portion emarginated; basal half with uniseriate macrosetae; plate surface with scattered microsetae; plates separate from each other throughout their length. Styles (Fig. 1e), in dorsal view, with apophysis short, not extending as far posteriorly as apex of connective, narrowing gradually toward apex, without preapical lobe, with few preapical setae on outer margin. Connective (Fig. 1e), in dorsal view, a large trapezoidal plate; without median keel. Aedeagus (Fig. 1f–g) symmetrical; shaft, in ventral view, expanded apically; in lateral view, with strong, median ventral process on basal half; shaft apex with pair of membranous lobes; shaft surface with pair of areas covered by small spines, extending from median ventral process to lateroapical area, where spines are larger than more basal ones. Paraphyses (Fig. 1h–i), in dorsal view, with both stalk and rami elongate, the former articulated with connective, the latter with apical half curved dorsally.

Females with abdominal sternite VII (Fig. 2a–b), in ventral view, strongly produced posteriorly; posterior margin with elongate, median strong projection and pair of elongate, but shorter than median projection, lateral spiniform processes; median projection with slight preapical constriction; ventral surface of sternite VII with distinct median longitudinal carina. Internal sternite VIII, in dorsal view, without distinct median or lateral sclerites. First valvifers (Fig. 2d), in lateral view, with anterior and dorsal margins rounded, ventral margin emarginated, posterior margin truncate. Pygofer (Fig. 2c), in lateral view, strongly produced posteriorly; apex narrowly rounded; ventral margin slightly emarginated preapically; macrosetae distributed mostly on posterior portion and extending anteriorly along ventral margin. First valvulae, in ventral view, with basal portion expanded, without processes or projections; in lateral view (Fig. 2d), with apex acute; dorsal margin with approximately 10 preapical denticles (Fig. 2g); dorsal

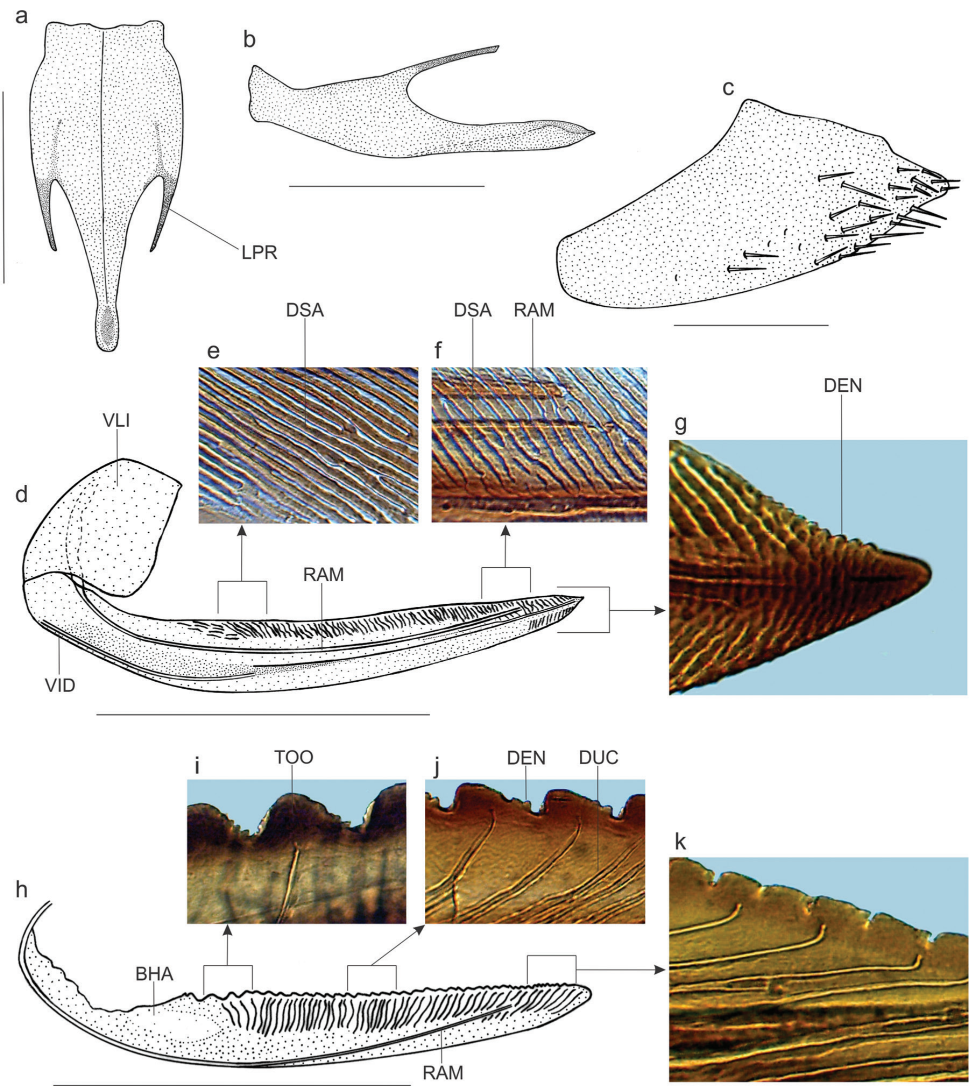

Figure 2. *Kogigonalia incarnata* (Germar, 1821), comb. n., female terminalia: **a** sternite VII, ventral view **b** sternite VII, lateral view **c** pygofer, lateral view **d** first valvifer and valvula, lateral view **e** dorsal sculptured area at basal portion **f** dorsal sculptured area at apical portion **g** apex **h** second valvula, lateral view **i** teeth at basal portion **j** teeth at median portion **k** teeth at apical portion. BHA = basal hyaline area; DEN = denticle; DSA = dorsal sculptured area; DUC = duct; LPR = lateral process of sternite VII; RAM = ramus; TOO = tooth; VID = ventral interlocking device; VLI = first valvifer. Scale bars: **a, b, d, h** = 2 mm, **c** = 1 mm.

sculptured area (Fig. 2e–f) extended from basal portion to apex of blade, formed mostly by oblique linear processes; ventral sculptured area restricted to apical portion of blade, formed mostly by scale-like processes; ventral interlocking device (Fig. 2d) restricted to basal half of blade, its apical third curved dorsally. Second valvulae (Fig. 2h), in

Figure 3. a–c color variation in *Kogigonalia incarnata* (Germar, 1821), comb. n., body, dorsal view: **a–b** male and female syntypes, respectively, from the state of Bahia, northeastern Brazil (Museum für Naturkunde, Universität Humboldt, Berlin) **c** female from Brazil **d–f** *K. enola* Young, 1977, male holotype from French Guiana (United States National Museum, Washington, D.C.): **d** body, dorsal view **e** paraphyses, dorsal view **f** aedeagus, lateral view. **a–d** reproduced, with permission, from Wilson et al. (2009) **e–f** redrawn from Young (1977). Scale bars = 5 mm.

lateral view, slightly expanded beyond basal curvature; basal hyaline area distinct; dorsal margin approximately rectilinear, with about 40 continuous teeth (Fig. 2i–k) that are progressively smaller toward apex; most teeth subtriangular but posterior ones quadrate;

few irregular denticles on posterior portion of larger teeth and on ventroapical portion of blade; ventral blade margin convex; without preapical prominence; apex obtuse. Gonoplacs, in lateral view, with basal half narrow and apical half distinctly expanded; apex obtuse; blade with many minute spiniform processes and few macrosetae on apical portion and extending anteriorly along ventral margin.

Material examined. northeastern Brazil: *state of Bahia*: one female (MTD). southeastern Brazil: *state of Espírito Santo*: one male, Santa Teresa, 675 m, 1–2/IV/1969, Exp. Dep. Zool. col. (DZUP); Baixo Guandu, 17/IX/1966, C. Elias col. (DZUP); *state of Rio de Janeiro*: two males and one female, Casimiro de Abreu, Reserva Biológica União, 28–31/I/2013 (one male), 12/XII/2013–27/I/2014 (one male, one female), Lab. Diptera MN[RJ] col., Malaise trap (MNRJ); one male, Silva Jardim, III/1974, F. M. Oliveira col. (DZUP); one male, Magé, 3/III/1978, J. L. Nessimian col. (DZRJ). Brazil: one female, D. Swainson col. (DZUP); one specimen without abdomen (MTD).

Key to males of *Kogigonalia* and female of *K. resoluta* (adapted from Young 1977)

Note: in addition to the present paper, the reader is referred to Young (1977, Figs 169-174) and Wilson et al. (2009) for illustrations and photographs of the external morphology and genital structures of *Kogigonalia* species that will be useful for evaluating the identifications obtained using our key.

1a	Dorsum red with a pair of yellow maculae on lateroposterior portions of crown and a pair of small yellow marks on lateral margins of pronotum .... ***K. resoluta* (Melichar, 1926)** (known only from female)	
1b	Dorsum not as above	**2**
2a	Aedeagus with a large, ventral unpaired process near midlength of shaft and no additional processes (Fig. 1f)	**3**
2b	Aedeagus without such a process or with additional processes	**4**
3a	Subgenital plates, in lateral view, extending approximately as far posteriorly as pygofer apex and, in ventral view, without outer emargination at transition from broad basal portion to narrow apical portion....	***K. enola* Young, 1977**
3b	Subgenital plates, in lateral view, very short, not extending as far posteriorly as pygofer apex and, in ventral view, with distinct outer emargination at transition from broad basal portion to narrow apical portion (Fig. 1c)	***K. incarnata* (Germar, 1821), comb. n.**
4a	Face with at least some black marking	**5**
4b	Face without black marking	**6**
5a	Genae yellow	***K. spectabilis* (Melichar, 1932)**
5b	Genae black	***K. zarumoidea* Young, 1977**
6a	Pygofer without processes; paraphyses present	***K. dietzi* Young, 1977**
6b	Pygofer with a process arising at middle of posterior margin; paraphyses absent	***K. cajana* Young, 1977**

Discussion

The aedeagus and paraphyses of *K. incarnata* are very similar to those of *K. enola*, a species described by Young (1977) from French Guiana. In these species, the aedeagus bears a large, ventral unpaired process near the midlength of shaft (Figs 1f, 3f) and the paraphyses have both the stalk and rami elongate (Figs 1h–i, 3e). Our assignment of *Tettigonia incarnata* to *Kogigonalia* is based mostly on these remarkable similarities. In addition, the color pattern of the forewings of *K. enola* (Fig. 3d) is very similar to that of *K. incarnata* (Fig. 3c) specimens that have three large orange or yellow areas on each wing. However, *K. incarnata* shows a great deal of intraspecific color variation; the orange or yellow forewing areas vary from distinct to faint or even absent (Fig. 3a–c); the dark marks of crown and pronotum are also variable, even between the syntype specimens from the state of Bahia, northeastern Brazil (Fig. 3a–b). In spite of this color variation, we believe that all specimens herein examined belong in *K. incarnata* because all males have the same genitalia morphology (Fig. 1b–i) and some of them match perfectly the color pattern of the syntypes. Likewise, females with distinct color patterns show the same terminalia morphology, including the strongly produced sternite VII (Fig. 2a–b). Similar cases of intraspecific color variation are known in other Cicadellini [e.g., *Macugonalia leucomelas* (Walker, 1851), *Tettisama quinquemaculata* (Germar, 1821), *Versigonalia ruficauda* (Walker, 1851)] and in Proconiini [e.g., *Pseudometopia amblardii* (Signoret, 1855), *Raphirhinus phosphoreus* (Linnaeus, 1758), *Teletusa limpida* (Signoret, 1855)].

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Michael Wilson (National Museum Wales) kindly gave us permission to use the photographs of the body of *K. incarnata* and *K. enola*. GM and RRC have fellowships from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, processes number 301391/2011-4 and 303127/2010-4, respectively). RSS has a fellowship for doctoral studies from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and VQ has a fellowship for undergraduate studies (PIBIC) from CNPq. This study was supported in part by Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) (grant number E-26/111.181/2011 to Nelson Ferreira-Jr – Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, UFRJ). Useful comments on the manuscript were provided by Stuart McKamey (National Museum of Natural History, Washington, D.C.), Daniela M. Takiya (UFRJ), and Rachel A. Carvalho (UFRJ).

References

Blanchard É (1840) Histoire naturelle des insectes: Orthoptères, Névroptères, Hémiptères, Hyménoptères, Lépidoptères et Diptères. Tome troisieme. Paris, P. Duméril, 672 pp. doi: 10.5962/bhl.title.59226

Germar EF (1821) Bemerkungen über einige Gattungen der Cicadarien. Magazin der Entomologie 4: 1–106.

Hamilton KGA (1981) Morphology and evolution of the rhynchotan head (Insecta: Hemiptera, Homoptera). Canadian Entomologist 113: 953–974. doi: 10.4039/Ent113953-11

Hill BG (1970) Comparative morphological study of selected higher categories of leafhoppers (Homoptera: Cicadellidae). University Microfilms, Ann Arbor, xi + 187 pp.

Holovachov OV (2008) Insects of E.-F. Germar in the collections of the Zoological Museum. http://zoomus.lviv.ua/en/germar_collection/ [accessed 9 December 2014]

McKamey SH (2007) Taxonomic catalogue of the leafhoppers (Membracoidea). Part 1. Cicadellinae. Memoirs of the American Entomological Institute 78: 1–394.

Mejdalani G (1993) Morfologia da cabeça de *Versigonalia ruficauda* (Walker, 1851), com notas sobre a terminologia (Homoptera, Cicadellidae, Cicadellinae). Revista Brasileira de Entomologia 37: 279–288.

Mejdalani G (1998) Morfologia externa dos Cicadellinae (Homoptera, Cicadellidae): comparação entre *Versigonalia ruficauda* (Walker) (Cicadellini) e *Tretogonia cribrata* Melichar (Proconiini), com notas sobre outras espécies e análise da terminologia. Revista Brasileira de Zoologia 15: 451–544. doi: 10.1590/S0101-81751998000200015

Metcalf ZP (1965) General catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Part 1, Tettigellidae. Agricultural Research Service, United States Department of Agriculture, Washington, D.C., 730 pp.

Nielson MW (1965) A revision of the genus *Cuerna* (Homoptera, Cicadellidae). Technical Bulletin of the United States Department of Agriculture 1318: 1–48.

Oman PW (1949) The Nearctic leafhoppers (Homoptera: Cicadellidae). A generic classification and check list. Memoirs of the Entomological Society of Washington 3: 1–253.

Shydlovskyy IV, Holovachov OV (2005) Homopteran insects from the collection of E.-F. Germar in the Zoological Museum of LNU (catalogue). Ivan Franko LNU Publishing, Lviv, VI+80 pp.

Signoret V (1853) Revue iconographique des Tettigonides. Annales de la Société Entomologique de France 1: 661–688, pls 21–22.

Wilson MR, Turner JA, McKamey SH (2009) Sharpshooter leafhoppers of the world (Hemiptera: Cicadellidae subfamily Cicadellinae). National Museum Wales. http://naturalhistory.museumwales.ac.uk/sharpshooters/home.php [accessed 22 October 2014]

Young DA (1977) Taxonomic study of the Cicadellinae (Homoptera: Cicadellidae). Part 2. New World Cicadellini and the genus *Cicadella*. Bulletin of North Carolina Agricultural Experiment Station 239: vi + 1135 pp.

Young DA, Beirne BP (1958) A taxonomic revision of the leafhopper genus *Flexamia* and a new related genus (Homoptera: Cicadellidae). Technical Bulletin of the United States Department of Agriculture 1173: 1–53.

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First record of the genus *Prosopistoma* Latreille, 1833 (Ephemeroptera, Prosopistomatidae) in Taiwan

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Abstract

The finding of three immature nymphs of *Prosopistoma* Latreille, 1833 (Ephemeroptera, Prosopistomatidae) in an upstream site of Baishih River represents the first record of this rarely collected genus in Taiwan. These nymphs were discovered through extensive monthly sampling at the riffle habitats from 13 undisturbed sites over two years (Dec 2008–Nov 2010). The coloration pattern of the collected immature nymphs in Taiwan is similar to the immature stage of *P. ocellatum* and *P. annamense*, two species which have been found in similarly undisturbed, upland forested-stream habitats.

Keywords

Mayfly, Prosopistomatidae, new record, nymph, morphology, Taiwan

Introduction

The Prosopistomatidae is a monogeneric family of Ephemeroptera, and is considered as rarely collected. At present, more than 20 known species of *Prosopistoma* Latreille, 1833 have been described from the Palaearctic, Oriental, Australasian, and Afrotropical regions (see review by Barber-James 2009, Shi and Tong 2013). The Oriental region (12 species) represents the most species-rich area for this genus (Lieftinck 1932, Peters 1967, Liu et al. 1984, Soldán and Braasch 1984, Tong and Dudgeon 2000, Sartori and Gattolliat 2003, Zhou and Zheng 2004, Barber-James et al. 2008, Barber-James 2009, Shi and Tong 2013). No *Prosopistoma* has been mentioned in Taiwan despite records of this genus in the nearby continental China and other major Asian Pacific islands (e.g. Philippines, Borneo, Java and Sumatra).

Studies on the diversity of mayfly in Taiwan started from Ulmer (1912) who mentioned nine species with decription of four new species of *Ephemera*, *Isonychia* and *Ecdyonurus*. The taxonomic records of mayfly extensively increased in 1990's (e.g. Kang and Yang 1994a, b, c, d, e, 1995, 1996a, b, Kang et al. 1994, Bae 1997) when 45 species of Ameletidae, Baetidae, Heptageniidae, Leptophlebiidae and Caenidae were described from more than 100 localities (see review in Soldán and Yang 2003). To date, at least 65 species (28 genera and 9 families) of mayflies are recorded in Taiwan (Soldán and Yang 2003). However, no *Prosopistoma* has been discovered in Taiwan in the last >100 years of entomological studies, suggesting its rarity in Taiwan. The present study is to report the first record of *Prosopistoma* in Taiwan and consequently its geographic extension in the Oriental region.

Materials and methods

Extensive monthly surveys for benthic macroinvertebrates at the riffle habitats from 13 undisturbed, upland sites of the Baishih River from the Water Resource Protection Area of the Feitsui Reservoir in New Taipei City, Taiwan were conducted for two years from Dec 2008 to Nov 2010 (Fig. 1). *Prosopistoma* nymphs were only discovered at the study site BA1 (Fig. 2), and samples were collected using hand nets from the stony streambed. All materials were collected by the author, and preserved in 95% ethanol. The specimens were examined and dissected under stereomicroscopes. The dissected mouthparts and legs were investigated using a compound light microscope. One specimens were air-dried, gold coated and examined using a Scanning Electron Microscope. All specimens are kept in the Ecology and Conservation Laboratory, Department of Bioenvironmental Systems Engineering, National Taiwan University, Taiwan (ECL). Terminology follows Kluge (2004) and Barber-James (2010).

Taxonomy

Family Prosopistomatidae Lameere, 1917
Genus *Prosopistoma* Latreille, 1833

***Prosopistoma* sp.**
Figs 3–6

Material examined. ECL-20100701-1: 1 nymph, TAIWAN, Baishih River (24.882695°N, 121.656242°E), 1.vii.2010. ECL-20100707-2: 1 nymph, TAIWAN,

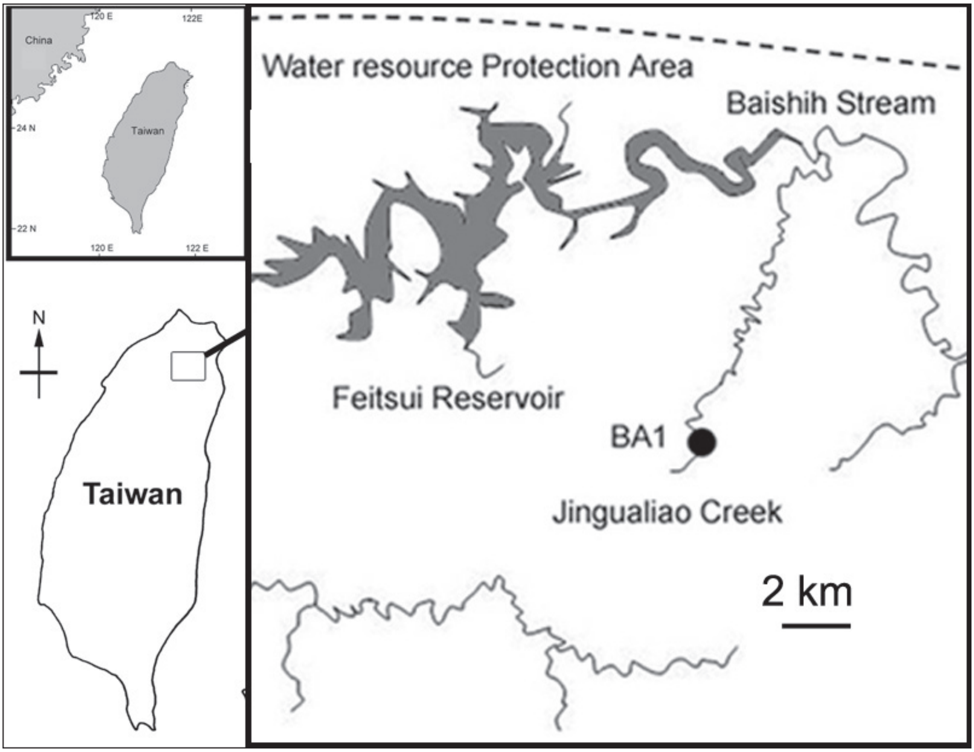

Figure 1. Map of Taiwan showing location of the study area. BA1 represents the collection site for *Prosopistoma* sp.

Figure 2. Photograph of the collection site BA1.

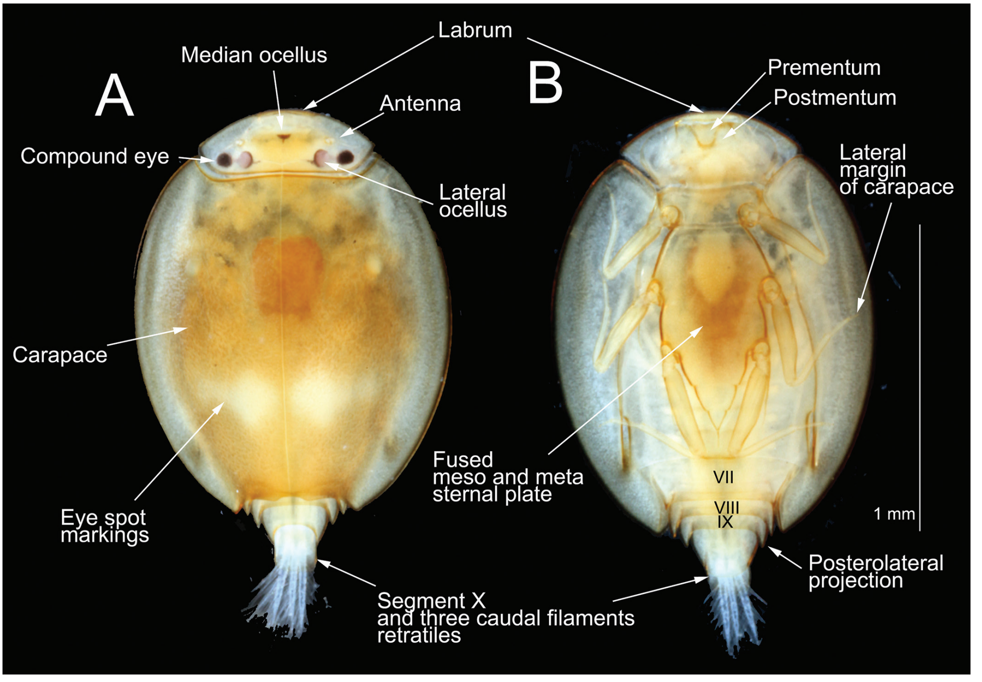

Figure 3. *Prosopistoma* sp. whole nymph: **A** Dorsal view **B** Ventral view.

Baishih River (24.882695°N, 121.656242°E), 7.vii.2010. ECL-20100707-3: same data as ECL-20100707-2.

Description. Immature nymph. Body length 1.5–2 mm, excluding caudal filaments. Head yellowish with a small red median ocellus, width about 3 times longer than length. Carapace coloration orange, with two white eye-spot markings on each side close to the mid line, about 2/3 of the distance from the base of the head. Distal end of carapace with a concave exhalent notch (Fig. 3A–B).

Head. Antenna with 5 segments, segment III longest (Fig. 4A). Labrum narrow, 3 times wider than long, surface with stout setae, anterior margin with sparse setae (Fig. 4B). Left and right mandibles similar, outer canine longer than the inner one, outer canine with three apical teeth, outer tooth the smallest with smooth outer margin, inner tooth the largest, with three short spines along the inner margin. Inner canine with two apical teeth, inner tooth larger with outer margin smooth, inner margin with two small spines. Two smooth setae below the inner tooth (Figs.4C–D). A single simple seta present lateromedially on each mandible (Fig. 4C). Maxillae with1 rigid canine at tip, with 3 subequal dentisetae and 3 stout setae (Fig. 4E–F). A simple seta at 2/3 of the sclerotized section of galea-lacinia (Fig. 4E-F). Maxillary palp 3-segmented, with segment II the longest (Fig. 4E). Labium composed of prementum and postmentum. Prementum trapezoid, cutting edge with fine teeth (Fig. 4G). Postmentum with large notch, to house the prementum (Fig. 4H). Labial palp 3-segmented, with the second the longest (Fig. 4G).

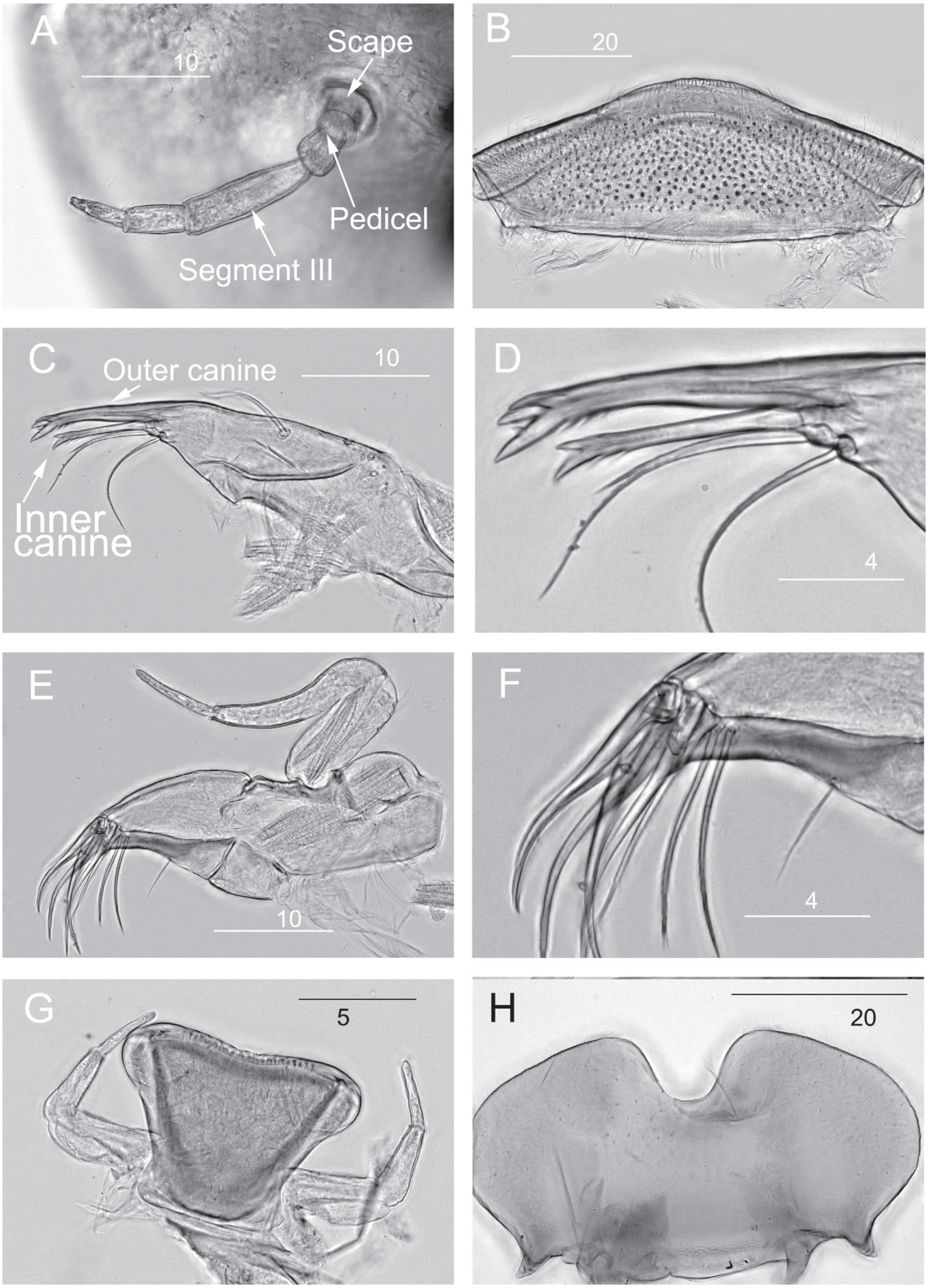

Figure 4. *Prosopistoma* sp.: **A** Antenna **B** Labrum **C** Mandible **D** Magnified view of inner and outer canine of mandible **E** Maxillae **F** Tip of Maxillae **G** Prementum with labial palps **H** postmentum. Scale bar in µm.

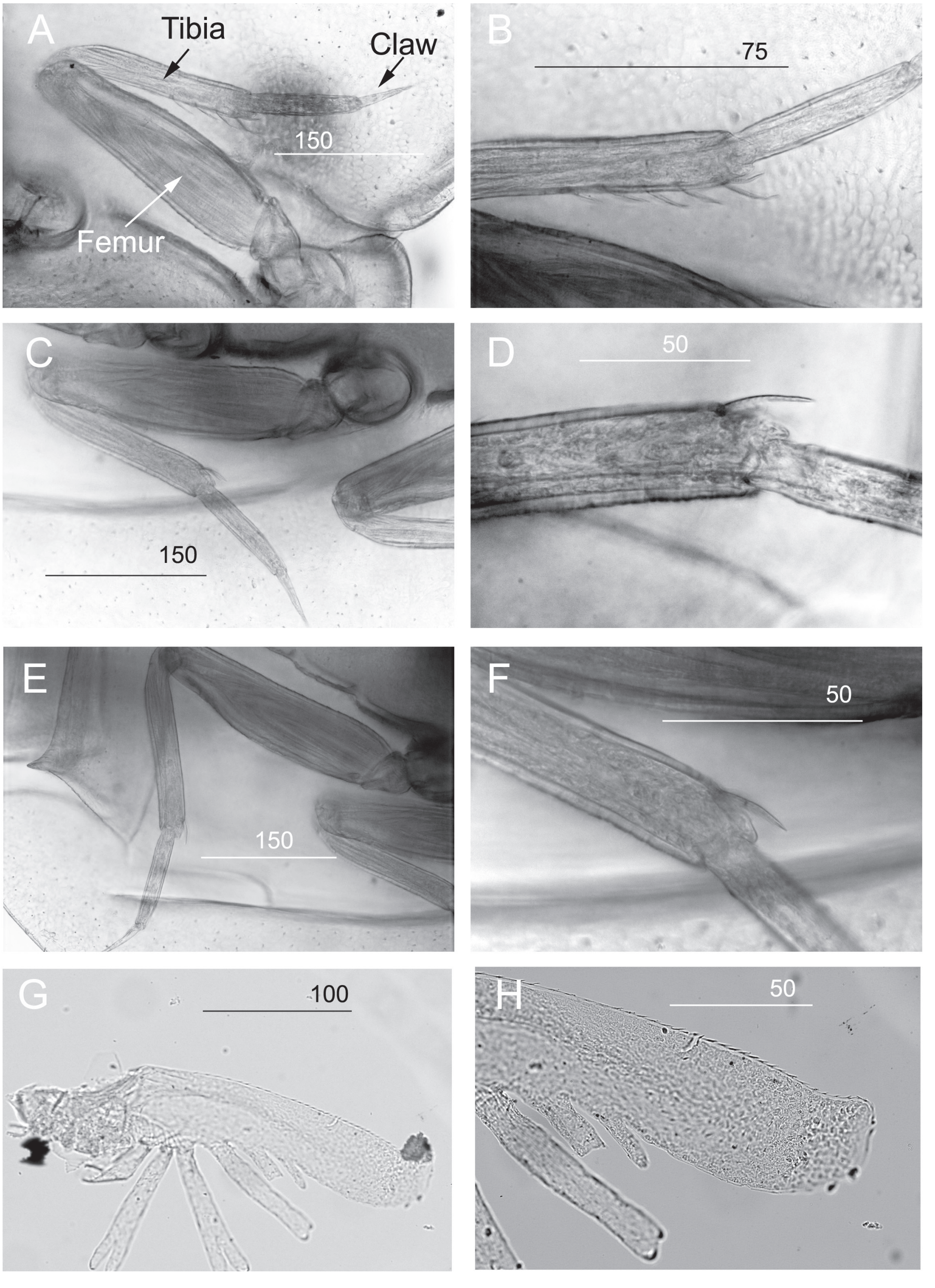

Figure 5. *Prosopistoma* sp.: **A** Leg I **B** Apex of ventral margin of tibia showing 4 serrated spines **C** Leg II **D** Apex of ventral margin of tibia of leg II **E** Leg III **F** Apex of ventral margin of tibia of leg III **G** Gill I **H** Upper lamellae portion of gill I. Scale bar in μm.

Legs. Dorsal and ventral margins of fore femur smooth (Figs 5A, 6A). Ventral margin of fore tibia with a row of 4 serrated setae (Figs 5B, 6C). Apical serrated setae on tibiae of legs II and III (Figs 5D, F, 6B, E–H). Claws of all legs sharp and without denticles (Fig. 6D).

Abdomen. Posterolateral projections of abdominal segments VII-IX sharp and with pointed apex (Fig. 3B). Three caudal filaments short and setose (Fig. 3B). Gill I with long upper lamellate portions, lamellate margin serrated, lower portions divided into several branches (Fig. 5G–H). Gill II leaf-like unbranched. Gill VI tiny, unbranched.

Distribution. At present, this unnamed species is only recorded in Baishih River from Taiwan.

Habitat. The collection site BA1 is an undisturbed forested-stream (356 m a.s.l., Fig. 2) with wetted width (6.3–10.5 m) and depth (0.2–0.7 m) relatively constant throughout the year. This site is generally oligotrophic (nitrate-nitrogen < 0.01 mg/L, ammonium-nitrogen = 1.40±0.28 mg/L, total phosphorus = 0.10±0.06 mg/L). Nymphs were found within the riffles with accumulated leaf packs on the bed substrates dominated by gravels and pebbles, moderate to high current velocity (26.7–65.1 cm/s) and high dissolved oxygen level (7.3–9.6 mg/L). Nymphs were rare and they contribute to the relative composition of the mayfly community by 0.19% during the study period. Dominant families of mayfly nymphs collected in the same habitat included Baetidae, Heptageniidae, Leptophlebiidae and Caenidae.

Remarks. According to the diagnostic key in Shi and Tong (2013), the immature nymphs of *Prosopistoma* sp. are morphologically similar to *P. ocellatum*. The coloration pattern of the collected immature nymphs in Taiwan is similar to the immature stage of *P. ocellatum* and *P. annamense*. However, as the important diagnostic characteristics, such as number of setae on fore tibia and number of antennal segments, are likely to change with ontogenetic shift, we cannot properly diagnose our specimens due to the lack of mature nymphs collected through extensive sampling in the present study.

Habitat of the nymphs of *Prosopistoma* sp. are similar to most *Prosopistoma* such as *P. annamense*, *P. olympus* and *P. ocellatum*. Their habitats are generally located in the undisturbed upstream site (altitude = 200–800 m a.s.l.) commonly characterized by stony streambed, shallow water depth, and moderate to high current velocity (Soldán and Braasch 1984, Sartori and Gattolliat 2003, Shi and Tong 2013) except that nymphs of *P. annamense* were recorded in the large urban river Xiangjiang from China (Liu et al. 1984).

In this study, the finding of three immature nymphs of *Prosopistoma* sp. from the upstream site of Baishih River represents the first record of this rarely collected genus in Taiwan. Thus, further collections should be conducted at more river sites to obtain the mature nymphs to ascertain the taxonomic status of this *Prosopistoma* sp. in Taiwan.

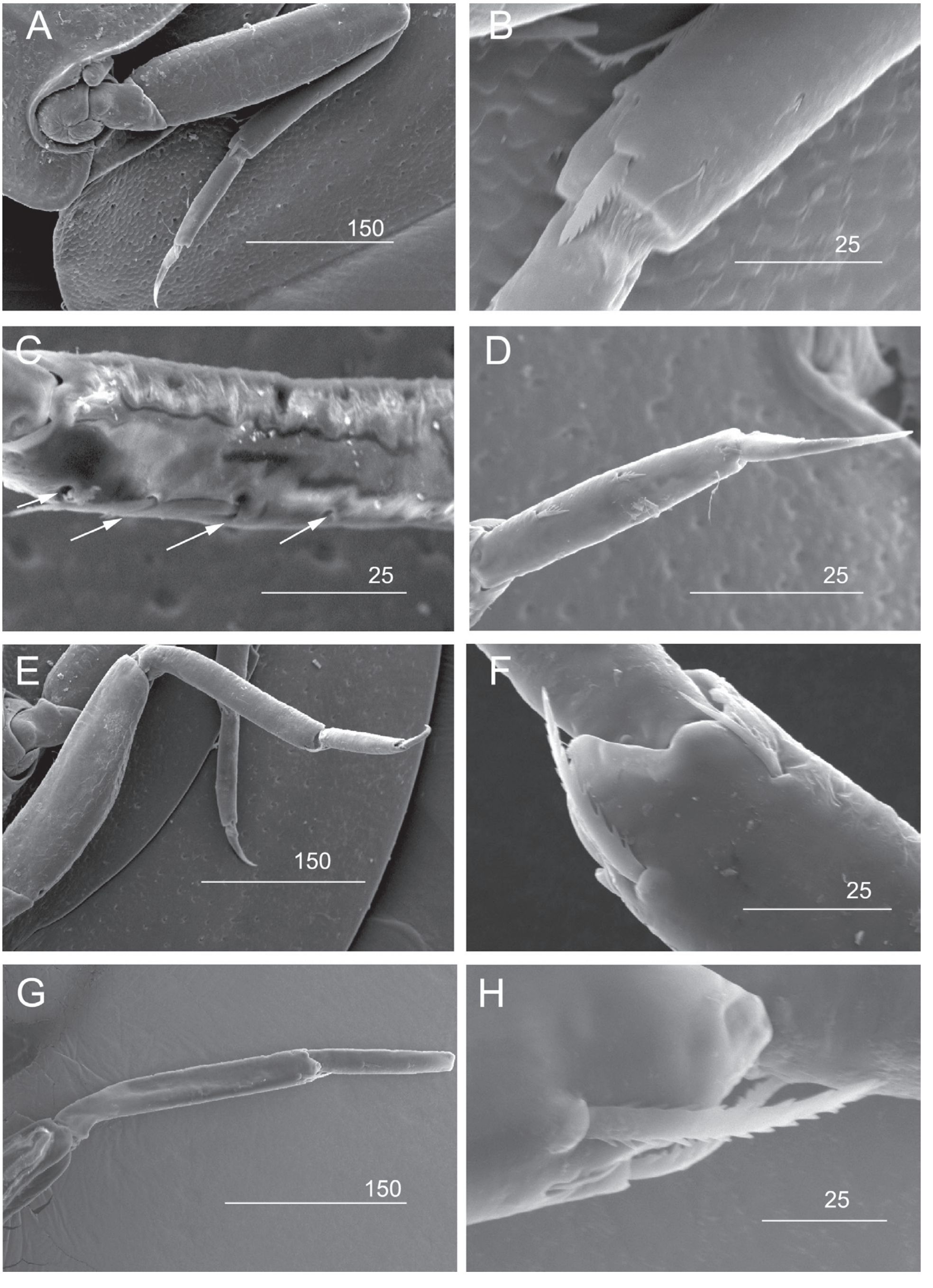

Figure 6. SEM of *Prosopistoma* sp.: **A** Leg I **B** Dorsal margin of tibia of leg I **C** Ventral margin of tibia of leg I, showing 4 serrated spines (indicated by white arrows). Note spines 1 and 4 are broken **D** Claw of leg I **E** Leg II **F** Fore-tibia of leg II **G** Leg III **H** Apex of fore-tibia of leg III. Scale bar in μm.

Acknowledgements

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References

Bae YJ (1997) A historical review of Ephemeroptera systematics in the Northeast Asia. In: Landolt P, Sartori M (Eds) Ephemeroptera & Plecoptera: Biology-Ecology-Systematics. MTL, Fribourg, 405–417.

Barber-James HM, Gattolliat JL, Sartori M, Hubbard MD (2008) Global diversity of mayflies (Ephemeroptera, Insecta) in freshwater. Hydrobiologia 59: 339–350. doi: 10.1007/s10750-007-9028-y

Barber-James HM (2009) A preliminary phylogeny of Prosopistomatidae (Ephemeroptera) based on morphological characters of the larvae, and an assessment of their distribution. Aquatic Insects 31: 149–166. doi: 10.1080/01650420903020502

Barber-James HM (2010) Neotype erection, redescription of the larva and first description of the winged stages of *Prosopistoma variegatum* Latreille, 1833 (Insecta: Ephemeroptera) from Madagascar. Aquatic Insects 32: 215–243. doi: 10.1080/01650424.2010.506691

Kang SC, Chang HC, Yang CT (1994) A revision of the genus *Baetis* in Taiwan (Ephemeroptera, Baetidae). Journal of Taiwan Museum 47: 9–44.

Kang SC, Yang CT (1994a) The nymph of *Isonychia formosana* (Ulmer, 1912) (Ephemeroptera, Oligoneuriidae). Journal of Taiwan Museum 47: 1–3.

Kang SC, Yang CT (1994b) Heptageniidae of Taiwan (Ephemeroptera). Journal of Taiwan Museum 1: 5–36.

Kang SC, Yang CT (1994c) Leptophlebiidae of Taiwan (Ephemeroptera). Journal of Taiwan Museum 47: 57–82.

Kang SC, Yang CT (1994d) Three new species of the genus *Ameletus* from Taiwan (Ephemeroptera: Siphlonuridae). Chinese Journal of Entomology 14: 261–269.

Kang SC, Yang CT (1994e) Ephemeroidea of Taiwan (Ephemeroptera). Chinese Journal of Entomology 14: 391–399.

Kang SC, Yang CT (1995) Ephemerellidae of Taiwan (Insecta, Ephemeroptera). Bulletin of the National Museum of Nature and Science 5: 95–116.

Kang SC, Yang CT (1996a) Two new species of *Baetis* Leach (Ephemeroptera: Baetidae) from Taiwan. Chinese Journal of Entomology 16: 61–66.

Kang SC, Yang CT (1996b) A new species of *Caenis* Stephens (Ephemeroptera: Caenidae) from Taiwan. Chinese Journal of Entomology 16: 55–59.

Kluge NJ (2004) The Phylogenetic System of Ephemeroptera. Kluwer Academia Publishers, Dordrecht, 442 pp. doi: 10.1007/978-94-007-0872-3

Lieftinck MA (1932) A new species of *Prosopistoma* from the Malay Archipelago (Ephemeropt.). Tijdschrift voor Entomologie (supplement) 75: 44–55.

Liu B, Wang S, Hu D (1984) An evaluation on pollution in the Xiang Jiang River by using zoobenthos. Acta Hydfrobiol Sin 8: 225–236.

Peters WL (1967) New species of *Prosopistoma* from the Oriental Region (Prosopistomatidae: Ephemeroptera). Tijdschrift voor Entomologie 110: 207–222.

Sartori M, Gattolliat JL (2003) First record and new species of the genus *Prosopistoma* Latreille, 1833 (Ephemeroptera, Prosopistomatidae) from Borneo (East Kalimantan, Indonesia). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 76: 301–305.

Shi W, Tong X (2013) A new species of *Prosopistoma* (Ephemeroptera: Prosopistomatidae) from China with a key to Oriental species. Zootaxa 3718: 89–096. doi: 10.11646/zootaxa.3718.1.8

Soldán T, Braasch D (1984) Two new species of the genus *Prosopistoma* (Ephemeroptera: Prosopistomatidae) from Vietnam. Acta Entomology of Bohemoslovaca 81: 370–376.

Soldán T, Yang JT (2003) Mayflies (Ephemeroptera) of Taiwan: Species composition, taxonomic shifts, distribution and biogeographical analysis. In: Gaino E (Ed.) Research Updates on Ephemeroptera and Plecoptera. Perugia, 413–419.

Tong XL, Dudgeon D (2000) A new species of *Prosopistoma* from China (Ephemeroptera: Prosopistomatidae). Aquatic Insects 22: 122–128. doi: 10.1076/0165-0424(200004)22:2;1-P;FT122

Ulmer G (1912) H. Sauter's Formosa-Ausbeute. Ephemeriden. Entomologische Mitteilungen 1: 369–375.

Zhou CF, Zheng LY (2004) The genus *Prosopistoma* from China, with descriptions of two new species (Ephemeroptera: Prosopistomatidae). Aquatic Insects 26: 3–8. doi: 10.1076/aqin.26.1.3.35375

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RESEARCH ARTICLE

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Integrative taxonomy reveals a new species of *Callisto* (Lepidoptera, Gracillariidae) in the Alps

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Abstract

Europe has one of the best-known Lepidopteran faunas in the world, yet many species are still being discovered, especially in groups of small moths. Here we describe a new gracillariid species from the south-eastern Alps, *Callisto basistrigella* Huemer, Deutsch & Triberti, **sp. n.** It shows differences from its sister species *C. coffeella* in morphology, the barcode region of the cytochrome *c* oxidase I gene and the nuclear gene histone H3. Both *C. basistrigella* and *C. coffeella* can co-occur in sympatry without evidence of admixture. Two *C. basistrigella* specimens show evidence of introgression. We highlight the importance of an integrative approach to delimit species, combining morphological and ecological data with mitochondrial and nuclear sequence data. Furthermore, in connection with this study, *Ornix blandella* Müller-Rutz, 1920, **syn. n.** is synonymized with *C. coffeella* (Zetterstedt, 1839).

Keywords

COI, DNA barcoding, histone H3, mitochondrial-nuclear discordance, leaf-mining moths, contact zone, new species

Introduction

Lepidoptera – butterflies and moths – are one of the most well-documented insect orders, but it is estimated that thousands of species, especially small-sized ones inhabiting the tropics, are still awaiting formal description. The integration of genetic data into taxonomic studies, especially with the advance of DNA barcoding campaigns (the construction of libraries of DNA barcodes for identification), has revealed many cases of cryptic or overlooked species in the tropics (Janzen et al. 2009, 2012), but also in some of the most studied regions such as Europe (Mutanen et al. 2012a, b, c, 2013).

Leaf-mining micro-moths in the family Gracillariidae are no exception. A study based on the analysis of DNA barcodes recently revealed a considerable number of undescribed species in the Neotropical region (Lees et al. 2013). In Europe, the systematics of this family is relatively well known, with 23 genera and 260 species recorded (De Prins and De Prins 2014) with new species still being discovered and described (Laštůvka and Laštůvka 2006, 2012; Triberti 2007; Laštůvka et al. 2013).

Here we focus on the gracillariid *Callisto coffeella* (Zetterstedt, 1839), an arctic-alpine species, which has been recorded from northern Europe, the Alps and a few other mountain areas of Europe. Its larvae initially mine leaves of several species of *Salix* and later feed in a folded leaf (Bengtsson and Johansson 2011). As all known *Callisto* species, *C. coffeella* adults have forewings with dark brown to blackish ground color with silvery white, oblique streaks (Figs 1–4). Due to these conspicuous wing markings they are relatively easy to identify. The alpha taxonomy of European *Callisto* has been established for a long time, with *Callisto insperatella* (Nickerl, 1864) being the most recently described species.

In a recent DNA barcoding study, Huemer (2011) found two genetic lineages within *C. coffeella*: one lineage formed by Austrian individuals from northern and central Alps, and a second one consisting of Italian specimens from the Southern Alps. Members of these two lineages differ on the basal silvery line of the forewings, which is transverse in south-eastern Alpine populations but vertical in all other examined populations (Fennoscandia, Northern and Central Alps). However, the author in contrast to other morphologically well-defined congeners found no differences in male and female genitalia. On the basis of phenotypical and genetic differences, it was suggested by P. Huemer that the south-eastern Alpine populations might represent a different subspecies.

Here we present new genetic, distribution and morphological data that support the hypothesis that individuals of *C. coffeella* from the south-eastern Alps represent a distinct lineage that we formally describe as a new species – *Callisto basistrigella* Huemer, Deutsch & Triberti, sp. n.

Materials and methods

Collections

Specimens examined in this study were obtained by rearing adults from leaf mines and by collecting adults flying by day around *Salix* bushes, mainly *S. glabra* Scop., 1772 and *S. waldsteiniana* Willd., 1806, but also a few *S. appendiculata* Villars, 1789 and *S. hastata* L., 1753. Some adults were collected at light trap or flew in the early morning hours. Data for all specimens studied morphologically and genetically can be found in the Suppl. material 1: Table S1.

Morphology

We examined the morphology of 135 dried, pinned and mostly set specimens belonging to *C. coffeella* s.l., the majority originating from the Alps, and half a dozen from Scandinavia. Pinned specimens were photographed with an Olympus E 3 digital camera and an Olympus SZX 10 binocular microscope, and processed with Helicon Focus 4.3 software, resulting in multiple images. Images were later edited by using Adobe Photoshop Lightroom 2.3 software. Genitalia were photographed with an Olympus E1 digital camera through an Olympus BH2 microscope.

Genitalia dissections and slide mounts followed Robinson (1976). Morphometric analysis was carried out on genital preparations of 16 adult males (5 from the southeastern alpine populations and 11 from Northern and Central alpine populations). Seven parameters were measured: phallus, valva, saccus, anellus and anellus process lengths, valva width and valva constriction.

All measurements were done on a Leica M 165C stereomicroscope by P. Triberti and expressed in mm. The dataset resulting from these measurements was analyzed using a multivariate approach – one-way ANOVA (Montgomery 2001), with species as a single categorical independent variable and the seven dependent measurement length variables mentioned above. Significance of each genital parameter was analyzed using a non-parametric Mann-Whitney test (MWT). Since our sampling size was rather small, particularly for southern populations, MWT was used because it does not require the normality of the data and allows tied values (Hollander and Wolfe 1999). With MWT, we tested the null hypothesis of no morphological differences. To avoid inter-correlations between dependent variables, we first estimated residual values of the correlated parameters using similar linear transformations (Draper and Smith 1998). We used this procedure for valva, saccus, and anellus process lengths, which were strongly correlated with phallus length. We used STATISTICA 8.0 (Stat Soft. Inc., USA) to conduct the analyses.

DNA sequence analysis

DNA extracts were prepared from a single hind leg removed from each of 21 specimens of *C. coffeella* s.l. DNA extraction, PCR amplification and sequencing of the barcode region were carried out at the Canadian Centre for DNA Barcoding (CCDB, Biodiversity Institute of Ontario, University of Guelph) following standard protocols (De Waard et al. 2008). In addition, 14 samples were processed at INRA (Orléans, France). DNA was extracted using QIAGEN DNeasy Blood & Tissue Kit according to the manufacturer's protocol. The COI barcoding fragment, 658 bp, was amplified via PCR using the primers LCO (5' GGT CAA CAA ATC ATA AAG ATA TTG G 3') and HCO (5' TAA ACT TCA GGG TGA CCA AAA AAT CA 3') and following standard conditions for the reaction (Folmer et al. 1994). PCR products were purified using the QIAGENAquick PCR purification kit and after used for the cycle sequencing reaction with Big Dye 3.1 (25 cycles of 35 min at 94 °C, 30 min at 46 °C and 1 min 30 sec at 72 °C).

Furthermore, 21 samples with DNA barcodes were also sequenced for the nuclear gene histone H3, a ~350 bp fragment, at INRA, Orléans. PCR for this gene was performed using primers Hex AF (5' -ATG GCT CGT ACC AAG CAG ACG GC -3') and Hex AR (5' -ATA TCC TTG GGC ATG ATG GTG AC-3') (Svenson and Whiting 2004) for 40 cycles (1 min at 94 °C, 1 min at 45 °C, 1 min at 65 °C and 10 min at 65 °C). Sequencing was carried out using a 3100 ABI genetic analyzer (Hitachi) with Big Dye 3.1 (25 cycles of 10 min at 96 °C, 5 min at 50 °C, 4 min at 60 °C). Both COI and histone H3 sequences were aligned using CodonCode Aligner 3.7.1. (CodonCode Corporation).

Sequence divergences were quantified using the Kimura 2-parameter model implemented within the analytical tools on BOLD (www.boldsystems.org) (Ratnasingham and Hebert 2007). A neighbor-joining (NJ) tree was constructed with MEGA 5.05 (Tamura et al. 2011). As a reference and to visually root the tree, we used one specimen of *Callisto insperatella* (Nickerl, 1864) (GRPAL094-10) for the COI tree and one specimen of *Parornix betulae* (Stainton, 1854) (GRACI621-10) for the histone H3 tree.

Specimen and sequence information

Details on the collecting data for each specimen, as well as a photograph of vouchers, sequence records, trace files, and primer sequences used for PCR amplification, together with GenBank accession numbers are available through the following dataset (http://dx.doi.org/10.5883/DS-CALLISTO) in BOLD (www.boldsystems.org).

Specimen depositories

LMK Landesmuseum Kärnten; Klagenfurt, Austria.
MCSN Museo Civico di Storia Naturale, Verona, Italy.
MCSNB Museo Civico di Scienze Naturali "E. Caffi", Bergamo, Italy.

SMNK Staatliches Museum für Naturkunde, Karlsruhe, Germany.
TLMF Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria.
UO University of Oulu, Finland.
VND inatura Erlebnis Naturschau Dornbirn, Austria.
ZSM Zoologische Staatssammlung, Munich, Germany.

Private collections

PCHD Helmut Deutsch, Bannberg, Assling, Tyrol, Austria.
PCJR Jurij Rekelj, Kranj, Slovenia.
PCJS Jürg Schmid, Illanz, Switzerland.
PCJW Josef Wimmer, Steyr, Austria.
PCJWdP Jurate and Willy De Prins, London, UK.
PCSG Stanislav Gomboc, Slovenia.

Results

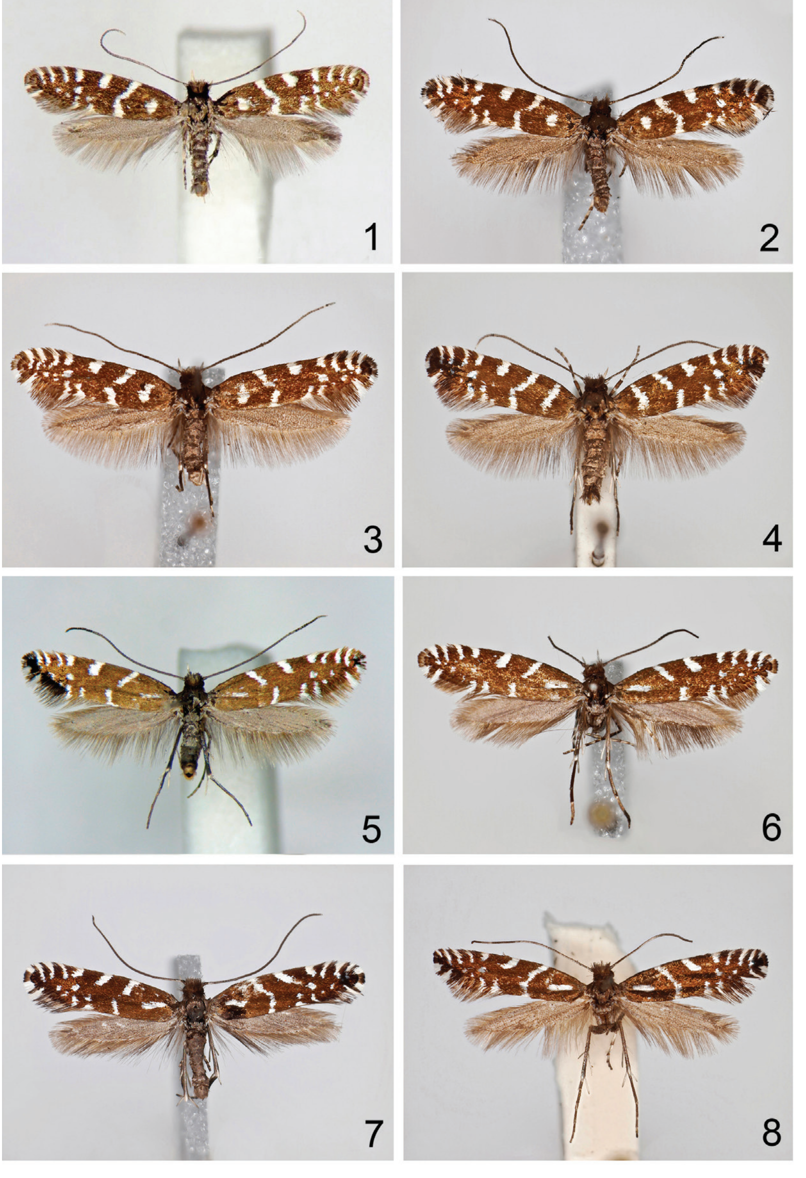
Morphology

Morphological analysis of the 135 specimens confirms the differences observed in wing pattern in the south-eastern alpine population. Eighty-two of these individuals were diagnosed as *Callisto coffeella* and 53 as the new species *C. basistrigella.* In addition, we detected two moths which morphologically corresponded to *C. basistrigella* but with a COI barcode they fell into the cluster of *C. coffeella* (see below Molecular divergences).

Callisto coffeella (Zetterstedt, 1839)

Oecophora coffeella Zetterstedt 1839: 1009.
Oecophora interruptella Zetterstedt 1839: 1009 [synonymised by Benander 1940: 61].
Ornix caelatella Zeller 1847: 585–586 [synonymised with *Oecophora interruptella* Zetterstedt, 1839 by Wocke (1862: 243)].
Ornix blandella Müller-Rutz 1920: 343. syn. n.
Annickia alpicola Gibeaux 1990: 23. [synonymised by Huemer 1990: 133].

Remarks. *Oecophora coffeella* was described from an unspecified number of male specimens collected on the 14th of July near Bjerkvik [according to original description ′Bjoerkvik" in Norwegian Lappland] (Zetterstedt 1839). *Oecophora interruptella* was described on the same page from a single male collected in 1836 in the Swedish province Dalarna, i.e. Dalecarlia by Boheman and from a female collected on 22nd of July 1812 near Gibostad, i.e. Giebostad, Norway. The type material was examined and figured by Benander (1940) who synonymized both taxa.



Figures 1–8. *Callisto* adults in dorsal view. **1** *C. coffeella*, male, Austria, Leitnertal, Oberer Stuckensee, 2150 m, 07.IX.2013, leg. Deutsch (PCHD) | voucher specimen № 3 | sample ID – NK318 | process ID CALCO003-14 **2** *C. coffeella*, male, Austria, Nordtirol, Bodenalpe, 2000 m, 9.–10.VII.1984, leg. Burmann (TLMF); **3** *C. coffeella*, male, Austria, Vorarlberg, Brandnertal, Böser Tritt, 1700-1800 m, 04.VII.1983, leg. Huemer (TLMF) **4** *C. coffeella*, female, Austria, Nordtirol, Obergurgl, 2000 m, e.l. M.III.1970, leg. Burmann (TLMF) **5** *C. basistrigella* sp. n., male, East Tyrol, Lienzer Dolomiten, Laserz, Dolomitenhütte, 1600 m, 12.VII.2013, leg. Deutsch (TLMF) | voucher specimen № 10 | sample ID – NK325 | process ID CALCO010-14 **6** *C. basistrigella* sp. n., male, Italy, Prov. Udine, Mte. Sernio, Forcella Nuviernulis, 1700 m, 16.VII.1988, leg. Huemer (TLMF) **7** *C. basistrigella* sp. n., male, Italy, Prov. Udine, Mt. Canin N, Rif. Gilberti, 1850–1950 m, 29.VII.2001, leg. Huemer (TLMF) **8** *C. basistrigella* sp. n., female, Italy, Prov. Udine, Montasio, 16.IX.1951, leg. Pinker (TLMF).

Annickia alpicola was described from a single male specimen collected in the French Alps (Gibeaux 1990) and later synonymized with *Callisto coffeella* by Huemer (1990).

Ornix caelatella was described from a single male collected in Montenero (Tuscany, Italy) in May by Josef Mann (Zeller 1847), later this species was synonymized with *Ornix interruptella* (= *Callisto coffeella*) by Wocke (1862). The whereabouts of the holotype is unknown but the detailed original description and the Mediterranean locality disagree with both *C. coffeella* and *C. basistrigella*. However, a further specimen from Styria (Austria), later determined by Zeller (1850) as *caelatella* but defined as a particular form, may be conspecific with *C. coffeella*. We conclude that *Ornix caelatella* is a dubious taxon until the holotype will be rediscovered.

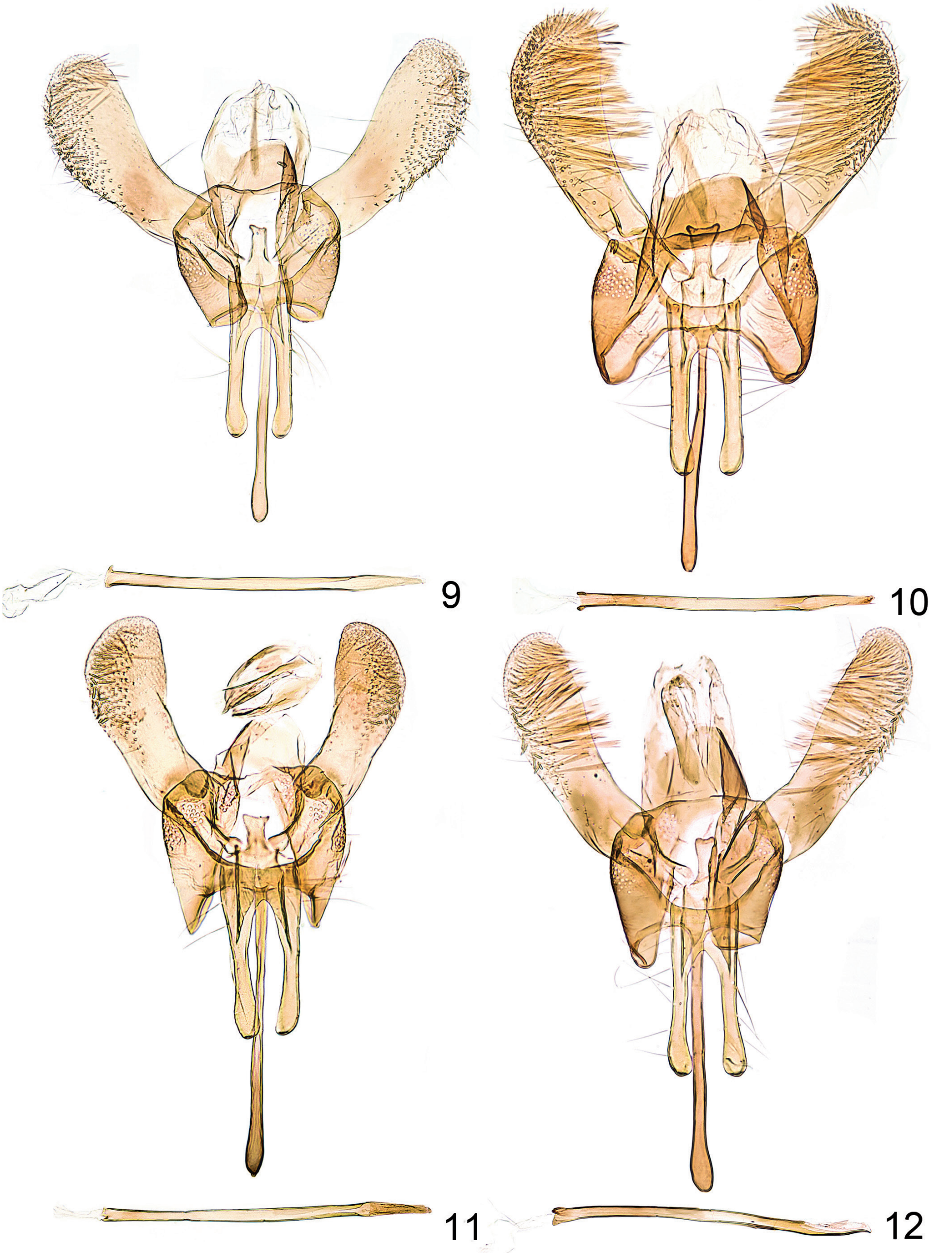
Ornix blandella was described by Müller-Rutz (1920) from a specimen bred by Paul Weber in Parpan (Switzerland) at 1500 m on *Salix* sp. Despite a focused search carried out by one of the authors (P. Triberti), the types were not found. However it was possible to study the original Müller-Rutz watercolours preserved in Naturhistorisches Museum Basel (Nr. 159 and 522) and they fully agree with typical *C. coffeella*. On the basis of what we conclude that *Ornix blandella* Müller-Rutz is a new synonym of *C. coffeella* Zetterstedt.

Description. Adult (Figs 1–4). Head dark brown, with distinct dark brown tuft of raised scales on vertex, frons lighter, greyish brown, labial palp cream. Wingspan 10–12 mm; forewing dark brown with distinct whitish silvery markings: transverse oblique sub-basal line showing sexual dimorphism, well developed from costa to fold in female (Fig. 4), shorter in male (Figs 1–3) and not extending to costa, rarely reduced to a spot in fold; angulate fascia at one third frequently separated into costal and tornal line; costa furthermore with short median strigula and two pairs of distal strigulae; dorsum with two small distal spots; small discal spot, supplemented by up to 2-3 spots distally; particularly distomedial spots silvery rather than whitish silvery; fringes with distinct cilia line, basal half darker than distal half, termen with two whitish spots; hindwing grey-brown with same-colour fringes.

Genitalia and eighth segment male (Figs 9–10, 13–14). Sternite 8 projected, bilobed. Tuba analis with long and thin subscaphium; valva slender, distally widened, with evenly rounded apex; vinculum laterally projected; saccus long and slender, rod-like, about as long as valva; anellus with pair of long and projecting processes; phallus slender, straight, about twice as long as valva, without distinct modifications, apically pointed.

Genitalia female (Fig. 17). Apophyses posteriors shorter than anteriores; segment 8 short, bare, intersegmental membrane to papillae anales very reduced; sterigma simple with ostium bursae wide, ventral margin medially more or less indented; antrum cup-shaped; ductus bursae moderately long and smooth, short sclerite just before antrum; corpus bursae, oval, longer than ductus bursae, signa formed by scobinations arranged in two longitudinal bands.

Distribution. The species is restricted to higher mountain areas and shows an arctic-alpine distribution pattern. According to various publications (i.e. Bengtsson and Johansson 2011, Heath and Emmet 1985, Huemer and Tarmann 1993, SwissLep-



Figures 9–12. *Callisto*, male genitalia. **9** *C. coffeella,* Vorarlberg Zürs, 1800 m, 29.VI.1939, leg. Burmann, gen. slide TIN 1 (TLMF) **10** *C. coffeella* Teriol sept., Vent 2000 m, e.l. 01.III.1956, leg. Burmann, gen. slide TIN 4 (TLMF) **11** *C. basistrigella* sp. n., Italia sept. Prov. Udine, Mte. Sernio, Forcella Nuviernulis 1700 m, 16.VII.1988 leg. Huemer gen. slide TIN 2 (TLMF) **12** *C. basistrigella* sp. n. Italia sept. Prov. Udine, Mte. Sernio, Forcella Nuviernulis 1700 m, 16.VII.1988 leg. Huemer gen. slide TIN 3(TLMF).

Team 2010) the species is locally distributed in the central and northern parts of Scandinavia, northern Scotland, and in the eastern, northern and central Alps. Most of these regions were included in our study, particularly alpine regions of Italy, Austria, Switzerland and Slovenia; sampling was also done in southeast of Germany and in Scandinavia (Norway, Sweden, Finland). In the Southern Alps it is known from a single record in France and from Aosta Valley to Carnic Alps in Italy. *Callisto coffeella* is also reported from Western Russia (Sinev 2008), Ukraine, Poland, Slovakia, and United Kingdom (De Prins and De Prins 2014) but we have been unable to check material from these countries.

Bionomics. The larval stage feeds on various species of mountainous *Salix* such as *Salix arbuscula* L., 1753 (which may refer to *S. arbuscula* in northern Europe or *S. waldsteiniana* in Central Europe), *S. phylicifolia* L., 1753 (Heath and Emmet 1985), *S. repens* L., 1753 (syn: *S. fusca*), *S. myrsinifolia* Salisb., 1796, *S. silesiaca* Willd., (1806) [basionym] (De Prins and De Prins 2014). In our study, *C. coffeella* was also reared from *Salix glabra*. Initially the larva produces a short epidermal gallery which suddenly widens to a blotch tentiform mine on the lower surface of a leaf, similar in appearance to mines of the genus *Phyllonorycter*. Later the mine is vacated and the larva forms a shelter along a leaf margin, folding an edge downwards as in many *Parornix*. Pupation takes place in a cocoon on the branch of the host-plant or in the laboratory between leaf litter and tissue. Hibernation occurs in the pupal stage. The adult is on the wing in June and July. It can be found during the day, most frequently in the morning and early evening flying around the hostplant. The species lives in montane and subalpine habitats of the dwarf-shrub zone both on calcareous and siliceous soil.

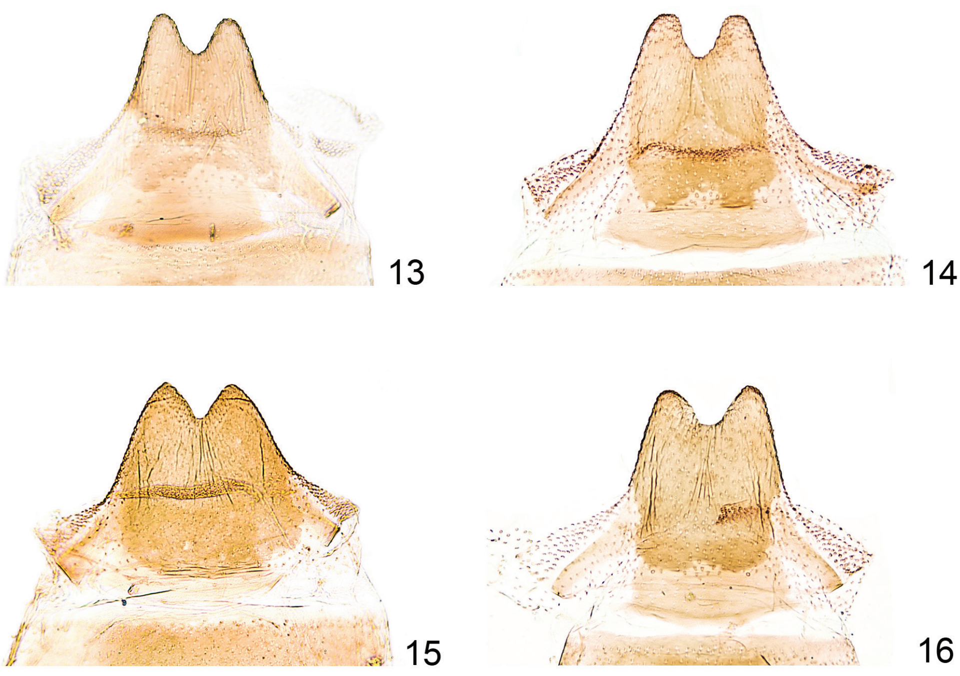
Callisto basistrigella **Huemer, Deutsch & Triberti, sp. n.**

http://zoobank.org/95B2011C-A39A-436E-8FF4-35ABEE5827E1

Type material. Holotype (Fig. 5): 1 male, East Tyrol, Lienzer Dolomiten, Laserz, Dolomitenhütte, 1600 m, 12.VII.2013, leg. Deutsch (TLMF) | voucher specimen № 10 | sample ID – NK325 | process ID CALCO010-14.

Paratypes. 33 males and 11 females.

Austria: 3 males, East Tyrol, Lienzer Dolomiten, Lavanter Almtal, 1200-1400 m, 07.VI.1998, leg. Deutsch (TLMF); 1 male, East Tyrol, Lienzer Dolomiten, Laserzgebiet, 1800-2000 m, 21.VI.1999, leg. Deutsch (TLMF); 1 male, East Tyrol, Carnic Alps, Leitnertal, Oberer Stuckensee, 2150 m, 14.VII.2013, leg. Deutsch (PCHD) | voucher specimen № 8 | sample ID – NK323 | process ID CALCO008-14; 2 males, East Tyrol, Carnic Alps, Leitnertal, Oberer Stuckensee, 2150 m, 07.IX.2013, leg. Deutsch (PCHD) | voucher specimens № 1 and № 2 | sample IDs – NK316 and NK317 | process Ids CALCO001-14 and CALCO002-14; 1 female, East Tyrol, Lienzer Dolomiten, Hochstadel, 2000 m, VII.1952, leg. Pinker (TLMF); 2 females, East Tyrol, Carnic Alps, Leitnertal, Oberer Stuckensee, 2150 m, 07.IX.2013, leg. Deutsch



Figures 13–16. *Callisto*, male, segment 8. **13** *C. coffeella,* Vorarlberg Zürs, 1800 m, 29.VI.1939, leg. Burmann, gen. slide TIN 1 (TLMF) **14** *C. coffeella,* Teriol sept., Vent 2000 m, e.l. 01.III.1956, leg. Burmann, gen. slide TIN 4 (TLMF) **15** *C. basistrigella* sp. n., Italia sept. Prov. Udine, Mte. Sernio, Forcella Nuviernulis 1700 m, 16.VII.1988, leg. Huemer, gen. slide TIN 2 (TLMF) **16** *C. basistrigella* sp. n., Italia sept. Prov. Udine, Mte. Sernio, Forcella Nuviernulis 1700 m, 16.VII.1988 leg. Huemer gen. slide TIN 3 (TLMF).

(PCHD) | voucher specimens № 4 and № 6 sample | sample IDs – NK319 and NK321 | process Ids CALCO004-14 and CALCO006-14.

Italy: 4 males, Prov. Belluno, Passo di Valparola E, 2200-2300 m, 20.VII.2009, leg. Huemer (TLMF); 1 female, same data but gen. slide TRB3893 and BC TLMF Lep 01801 (TLMF); 1 male, A. Carniche, Sappada, Casera Sesis, 1800 m, 12.VI. unknown year, leg. Rocca, gen. slide TRB 1778 (MCSN); 1 male, A. Carniche, Sappada, Passo Siera, 1600 m, 04.VII.1933, leg. Rocca, gen. slide TRB 1785 (MCSN); 1 male, A. Carniche, Sappada, Hosthaus, 1800 m, 14.VII.1936, leg. Rocca (MCSN); 2 males, 2 females, A. Carniche, Sappada, L. d'Olbe, 2000 m, 02.VII.1933, leg. Rocca, gen. slide TRB284 male, TRB3894 male (MCSN); 1 male, Prov. Udine, Mte. Sernio-Massiv Forcella Nuviernulis 1700 m, 16.VII.1988, leg. Huemer, GU TIN2 male P. Huemer 'Callisto coffeella Zett. det. Triberti' (TLMF); 1 male, Prov. Udine, Mte. Sernio-Massiv Forcella Nuviernulis 1700 m, 16.VII.1988, leg. Huemer, GU TIN3 male (TLMF); 1 male, 1 female, Prov. Udine, Montasio, 16.IX.1951, leg. Pinker, gen. slide TIN8 female (TLMF); 11 males, 1 female, Prov. Udine, Monte Canin N, Rif. Gilberti Umg., 1850-1950 m, 29.VII.2001, leg. Huemer (TLMF); 1 male, 1 female, Prov. Udine, Monte Canin, Biv. Marussich, 2040 m, 06.VII.2002, leg. Wieser (LMK); 3 males, Prov. Udine, Monte Canin, Sella di Grubia, 1700 m, 20.VI.2003, leg. Wieser (LMK).

Slovenia: 1 female, Crna Prst, 1400 m, 18.VII.1899, leg. Penther (TLMF).

Diagnosis. In external appearance *C. basistrigella* is distinguishable from *C. coffeella* by its forewing pattern. In *C. basistrigella*, the sub-basal whitish silvery line of the forewing is almost parallel and lies in the fold, whereas in *C. coffeella* this line is transverse to the wing axis or reduced to a spot. On average, the forewings are slightly narrower than in *C. coffeella* (visible in series). Sexual dimorphism, as observed in *C. coffeella*, is absent in *C. basistrigella*. Genitalia do not provide obvious diagnostic differences but the length of the phallus is significantly longer in *C. basistrigella* than in *C. coffeella* although more specimens would be needed to confirm this difference (see Genital morphometrics).

Description. Adult (Figs 5–8). Wingspan 10.5–13.0 mm; forewing in sub-basal area with longitudinal, slightly oblique, whitish silvery line in fold. Other characters as described above for *C. coffeella*. The angulate fascia at one third of forewing frequently separated into costal and tornal line.

Genitalia and subgenital segments male (Figs 11–12, 15–16). As described above for *C. coffeella*.

Genitalia female (Fig. 18). As described above for *C. coffeella*.

Distribution. Only known from a small area in the south-eastern Alps, ranging from the Dolomites (Italy) in the west to the Julian Alps (Slovenia) in the east and the Carnic Alps and Lienzer Dolomiten (Austria) in the north (Fig. 19A, B).

Etymology. The name refers to the characteristic wing markings.

Bionomics. Early stages are undescribed. Both *C. basistrigella* and *C. coffeella* adults have been collected during the day, flying around low bushes of alpine *Salix glabra* and *S. waldsteiniana*. The flight period is largely dependent on exposure and snow coverage and usually extends between early June and late July. Under extreme conditions such as harsh winters adults have been collected as late as mid-September. The habitats are related to the dwarf-shrub zone and include subalpine meadows, rock formations and scree with *Salix*-bushes and shrubs. *C. basistrigella* is restricted to limestone with an altitudinal range from about 1200 to 2300 m.

Genital morphometrics. Multivariate ANOVA analysis based on morphometric of seven genital characteristics of the male moths failed to find any significant difference between *C. coffeella* and *C. basistrigella* (*Wilks'* $\lambda = 0.36$, $F = 2.07$, $p = 0.16$). Six out of seven parameters, i.e valva, saccus, anellus and anellus process lengths, valva width and valva constriction were not found to differ in the two species. Non-parametric Mann-Whitney test however indicated that the phallus is significantly longer in *Callisto basistrigella* than in *C. coffeella* (MWT : $Z = 2.36$, $N = 16$, $p = 0.02$), although sample sizes remain relatively small (*C. basistrigella* N = 5, *C. coffeella* N = 11) (Fig. 20). Two specimens of *C. basistrigella* from Sappada (Italy) made significant contributions to phallus length value of the species, exceeding the averaged length of *C. coffeella* phallus by 27%.

Figures 17–18. *Callisto*, female genitalia. **17** *C. coffeella,* Austria, Vorarlberg, Brandnertal, Böser Tritt, 1700–1800 m, 02.VII.1983, leg. Huemer gen. slide TIN 9 (TLMF) **18** *C. basistrigella* sp. n., Prov. Udine, Montasio, 16.IX.1951, leg. Pinker gen. slide TIN 8 (TLMF).

Molecular divergences

DNA barcodes. We obtained DNA barcodes for 21 specimens of *C. coffeella* and 14 specimens of *C. basistrigella*. Their analysis revealed that the samples of these species form two distinct clusters in the NJ tree (Fig. 21A), with two exceptions: one Slovenian

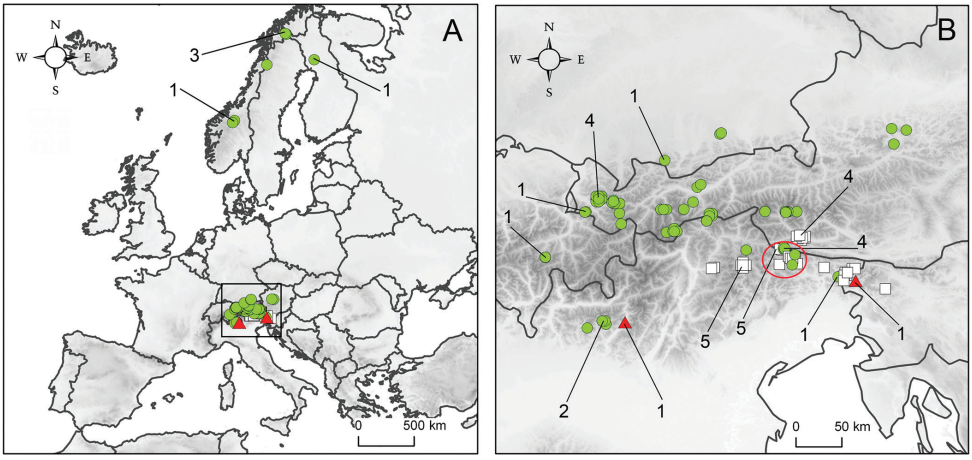


Figure 19. A sampling area of *Callisto coffeella* and *C. basistrigella* in Europe. **B** close up of the distribution of *C. coffeella* (green circles) and *C. basistrigella* (white squares) in the Alps; two *C. basistrigella* specimens (red triangles) show evidence of introgression. On Figs 19A, 19B, the 35 barcoded specimens are shown with numbers (1-5). The red circle on Fig. 19B shows the contact zone where both species occur together (Leitnertal, Eastern Tyrol, Austria and Sappada, Italy). When several samples were investigated per locality, the samples with the same coordinates have been slightly shifted in order to visualize overlapping data points on Fig. 19B.

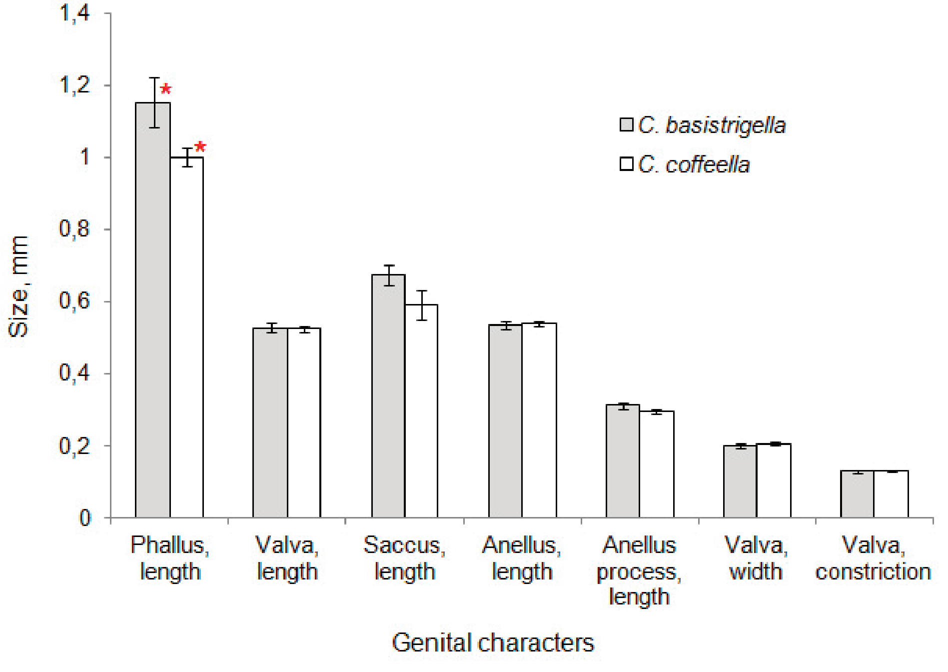


Figure 20. Genitalia measurements (mean values ± standard error) for the two *Callisto* species studied. The bars marked by an asterisk are significantly different from each other (MWT: $Z = 2.36$, $N = 16$, $p = 0.02$); in others cases, there is no difference between the species.

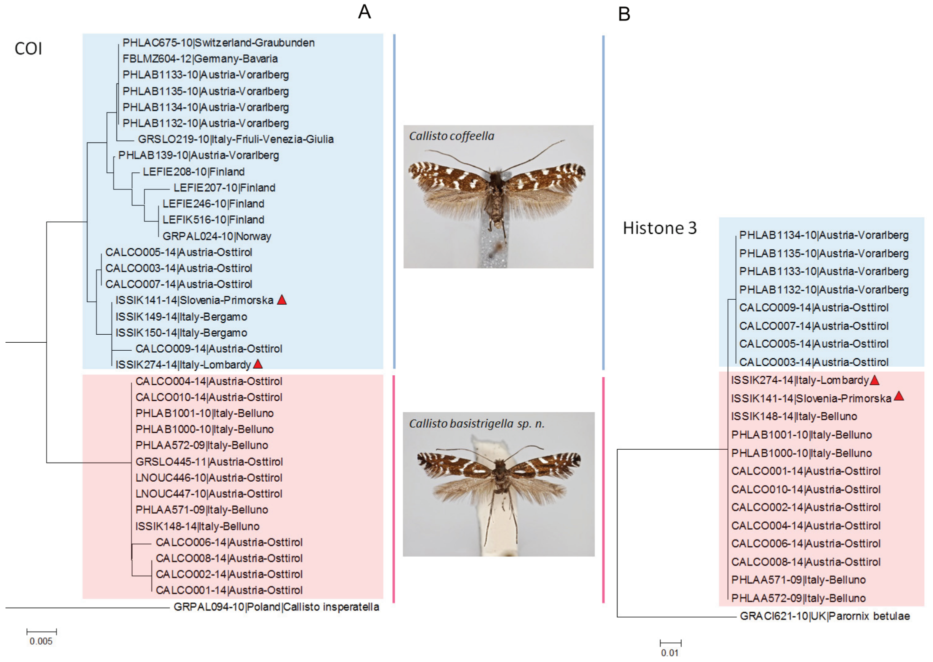


Figure 21. A neighbor joining tree based on the COI barcode fragment and **B** based on the histone H3 gene. The two specimens (ISSIK141-14, ISSIK274-14) with the *C. basistrigella* phenotype, but branching within the *C. coffeella* DNA barcode and within the *C. basistrigella* histone H3 cluster are marked with red triangles (as in Fig. 19) in both trees.

Table 1. Diagnostic substitutions in COI-DNA barcode sequences of *Callisto coffeella* and *C. basistrigella*.

Position	70	88	145	206	271	295	547	631
C. basistrigella	T	T	T	C	T	A	A	A
C. coffeella	A	A	C	T	C	C	C	G

(ISSIK141-14) and one Italian (ISSIK274-14) identified morphologically (and also by nuclear data, see below) as *C. basistrigella* grouped with *C. coffeella* (Fig. 21A), suggesting introgression or incomplete lineage sorting.

Excluding these two records, pairwise interspecific distances range between 1.39% and 2.37%, with a mean value of 1.75% (*sd* = 0.2). Within *C. basistrigella* and *C. coffeella*, respectively, genetic distances range from 0 to 0.31% (mean-value 0.17%, *sd* = 0.11) and from 0 to 1.23% (mean-value 0,56%, *sd* = 0.31). Sequence comparison revealed eight diagnostic substitutions (Table 1).

Histone H3. We obtained sequences of the nuclear gene histone H3 (328 bp) for the same 21 moths that were barcoded. H3 showed a high conservatism, with a single diagnostic nucleotide substitution at position 151, dividing the studied specimens into two clusters matching exactly the morphology-based separation of *C. coffeella* and *C. basistrigella* (Fig. 21B).

The Slovenian (ISSIK141-14) and Italian (ISSIK274-14) specimens, morphologically assigned to *C. basistrigella* and whose DNA barcodes clustered within *C. coffeella* (Fig. 21A), have histone H3 sequences identical to other *C. basistrigella* specimens (Fig. 21B).

Contact zone. Both *Callisto basistrigella* and *C. coffeella* were found to occur in the same localities in the Carnic Alps (Leitnertal, Eastern Tyrol, Austria) at the altitude up to 2150 m (Fig. 19). Out of 9 specimens collected in Leitnertal (1 *C. coffeella*, 1 *C. basistrigella* collected on 14.VII.2013, 2 *C. basistrigella* on 27.VII.2013, about 30 leaf mines on *Salix glabra* on 07.IX.2013), 4 specimens were identified based on both morphology and genetic data as *C. coffeella* and 5 specimens were identified as *C. basistrigella*. In addition, 7 of 9 samples (i.e. 3 specimens of *C. coffeella* and 4 of *C. basistrigella*) were reared from the same host plant – *Salix glabra*. Furthermore old records confirm this sympatry in the nearby Italian Carnic Alps, in the surroundings of Sappada (1 *C. coffeella* and 1 *C. basistrigella* were collected in Passo Siera, 1600 m, 04.VII.1933; 1 *C. coffeella* and 4 *C. basistrigella* – in L. d'Olbe, 2000 m, 02.VII.1933) (Fig. 19B). No evidence of genetic admixture was detected in the contact zone.

Discussion

Our study used newly generated mitochondrial and nuclear data in combination with morphological and morphometric data to characterize the variability of *Callisto coffeella* across its range. We confirmed the existence of two distinct lineages, one of which is described here as *C. basistrigella*. Its status as a distinct species is supported by morphology, nuclear DNA (histone H3 gene) and by mtDNA (COI-DNA barcodes), although shared haplotypes of the latter suggest introgression or incomplete lineage sorting.

Species delineation with DNA barcodes. In Lepidoptera, although authors generally reject the use of a threshold to delineate species, an empirical 2% (K2P) intraspecific distance value has often been proposed, pragmatically, as indicating "deep divergence" suggestive of potential overlooked or cryptic diversity (Hebert et al. 2010; Hausmann et al. 2011; Huemer et al. 2014; Rougerie et al. 2014). In the present study, we brought to the fore a case of overlooked species in which the DNA barcode divergence between the newly recognized pair of species can be as low as 1.39%; this case would then have been missed if the screening of our results had been based on the strict application of a 2% threshold before triggering further investigation. Furthermore, we reported two cases of nuclear/mitochondrial discordance in samples ISSIK141-14 and ISSIK274-14 (see Fig. 21) where histone H3 sequences and morphology conflict with the assignment based on DNA barcodes. This may have been caused by genetic introgression or incomplete lineage sorting. This finding is important as it highlights the necessary caution when using DNA barcodes for the identification of this and other pairs of closely related species. Whereas most specimens are likely to be correctly identified on the basis of this genetic marker (discordance was detected in two (5.7%) out of 35 specimens only), one should use characters of the wing pattern (or additional genetic data) to confirm identities where certain identification is needed.

Contact zone. We found that *Callisto basistrigella* occurs in sympatry with *C. coffeella* in the Carnic Alps, Leitnertal, 2150 m (East Tyrol, Austria) and Sappada 1600-1800 m (Italy), without evidence of admixture in this area. The two cases of nuclear/mitochondrial discordance revealed suggests possible genetic introgression between the two species. Further sampling and the use of fast evolving markers will be needed to investigate the course of a putative contact zone as well as the extent of gene flow between the two species.

Biogeography and speciation. The distribution of *C. basistrigella* as currently known is shared by several other endemic Lepidoptera. The south-eastern Alps is considered as one of the major areas of endemism in the region (Huemer 1998). However, most of the taxa restricted to this area have been defined only by morphological characters so far and their taxonomy has to be re-assessed using molecular data. The specific distinctness of *Udea murinalis* (Fischer von Röslerstamm, 1842) and the allopatric south-eastern alpine *Udea carniolica* Huemer & Tarmann, 1989 (Lepidoptera, Crambidae) both separated by moderate morphological differences, was recently well supported by molecular datasets (Mally and Nuss 2011). Another alleged set of sister taxa include *Dichrorampha bugnionana bugnionana* (Duponchel, 1843) and the south-eastern alpine subspecies *D. bugnionana dolomitana* Huemer, 1993 with a significant barcode divergence (Huemer unpublished data).

Allopatric isolation during the last glacial period is probably the main process by which *C. basistrigella* and *C. coffeella* diverged. Indeed, as many other cold-adapted Lepidoptera *C. coffeella* populations may have had a wide distribution in the periglacial tundra belts during the last glacial period. With increasing temperatures during the last interglacial period, *C. coffeella* may have moved northwards while southern populations moved up in altitude in the Alps (Mutanen et al. 2012c). On the other hand, *C. basistrigella* is restricted to the south-eastern Alps and may have derived from populations having occupied distinct refugia during the last glacial period.

Our results highlight the need to carry out additional intraspecific studies looking at patterns of both morphological and genetic variability within species across their ranges, which can reveal overlooked diversity and new species (Huemer 2011, Huemer and Mutanen 2012, Mutanen et al. 2012a–c), in regions that are thought to be well studied.

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References

Benander P (1940) Revision von Zetterstedt´s lappländischen Microlepidoptera. Opuscula entomologica 5: 49–65.

Bengtsson BÅ, Johansson R (2011) Nationalnyckeln till Sveriges flora och fauna. Fjärilar: Bronsmalar-rullvingemalar. Lepidoptera: Roeslerstammiidae-Lyonetiidae. ArtDatabanken, SLU, Uppsala, 494 pp.

De Prins J, De Prins W (2014) Global Taxonomic Database of Gracillariidae (Lepidoptera). World Wide Web electronic publication http://www.gracillariidae.net

De Waard JR, Ivanova NV, Hajibabaei M, Hebert PDN (2008) Assembling DNA barcodes: analytical methods. In: Cristofre M (Ed.) Methods in Molecular Biology: Environmental Genetics. Humana Press Inc., Totowa, USA, 275–293.

Draper NR, Smith H (1998) Applied regression analysis. Wiley series in Probability and Statistics. 3rd Edition. Wiley, 736 pp. doi: 10.1002/9781118625590

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.

Gibeaux C (1990) *Annickia alpicola* nov. gen., nov. sp. (Lepidoptera Tineidae Meessiinae). Entomologica gallica 2: 23–25.

Hausmann A, Haszprunar G, Hebert PDN (2011) DNA barcoding the geometrid fauna of Bavaria (Lepidoptera): Successes, surprises, and questions. PLoS ONE 6: e17134. doi: 10.1371/journal.pone.0017134

Heath J, Emmet MA (Eds) (1985) The moths and butterflies of Great Britain and Ireland. Vol. 2 Cossidae-Heliodinidae. Harley Books, Colchester, 460 pp.

Hebert PDN, DeWaard JR, Landry JF (2010) DNA barcodes for 1/1000 of the animal kingdom. Biology letters 6: 359–362. doi: 10.1098/rsbl.2009.0848

Hollander M, Wolfe DA (1999) Nonparametric Statistical Methods. John Wiley & Sons, New York.

Huemer P (1990) On the identity of *Annickia alpicola* Gibeaux, 1990 (Lepidoptera, Tineidae, Gracillariidae). Nota lepidopterologica 13: 133–136.

Huemer P (1998) Endemische Schmetterlinge der Alpen – ein Überblick (Lepidoptera). Stapfia 55: 229–256.

Huemer P (2011) Pseudo-endemism and cryptic diversity in Lepidoptera – case studies from the Alps and the Abruzzi. Journal on Protected Mountain Areas Research eco.mont 3: 11–18. doi: 10.1553/eco.mont-3-1s11

Huemer P, Karsholt O, Mutanen M (2014) DNA barcoding as a screening tool for cryptic diversity: an example from *Caryocolum*, with description of a new species (Lepidoptera, Gelechiidae). Zookeys 404: 91–111. doi: 10.3897/zookeys.404.7234

Huemer P, Mutanen M (2012) Taxonomy of spatially disjunct alpine *Teleiopsis albifemorella* s. lat. (Lepidoptera: Gelechiidae) revealed by molecular data and morphology – how many species are there? Zootaxa 3580: 1–23.

Huemer P, Tarmann G (1993) Die Schmetterlinge Österreichs (Lepidoptera). Systematisches Verzeichnis mit Verbreitungsangaben für die einzelnen Bundesländer. Veröffentlichungen des Museum Ferdinandeum, Suppl. 5, 224 pp.

Janzen DH, Hallwachs W, Blandin P, Burns JM, Cadiou J-M, Chacon I, Dapkey T, Deans A, Epstein M, Espinoza B et al. (2009) Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. Molecular Ecology Resources 9(s1): 1–26. doi: 10.1111/j.1755-0998.2009.02628.x

Janzen DH, Hallwachs W, Harvey DJ, Darrow K, Rougerie R, Hajibabaei M, Smith MA, Bertrand C, Gamboa IC, Espinoza B et al. (2012) What happens to the traditional taxonomy when a well-known tropical saturniid moth fauna is DNA barcoded? Invertebrate Systematics 26(6): 478. doi: 10.1071/IS12038

Laštůvka A, Laštůvka Z (2006) The European *Phyllonorycter* species feeding on the plants of the tribe Genisteae (Fabaceae), with descriptions of twelve new species (Lepidoptera: Gracillariidae). Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis 54(5): 65–84. doi: 10.11118/actaun200654050065

Laštůvka Z, Laštůvka A (2012) Additional data on the *Phyllonorycter haasi*-group with description of two new species (Lepidoptera: Gracillariidae). SHILAP Revista Lepidopterologia 40 (158): 231–239.

Laštůvka Z, Laštůvka A, Lopez-Vaamonde C (2013) A revision of the *Phyllonorycter ulicicolella* species group with description of a new species (Lepidoptera: Gracillariidae). SHILAP Revista Lepidopterologia 41(162): 251–265.

Lees DC, Kawahara AY, Bouteleux O, Ohshima I, Kawakita A, Rougerie R, De Prins J, Lopez-Vaamonde C (2013) DNA barcoding reveals a largely unknown fauna of Gracillariidae leaf-mining moths in the Neotropics. Molecular Ecology Resources 14(2): 286–296. doi: 10.1111/1755-0998.12178

Mally R, Nuss M (2011) Molecular and morphological phylogeny of European *Udea* moths (Insecta: Lepidoptera: Pyraloidea). Arthropod Systematics and Phylogeny 69: 55–71.

Montgomery DC (2001) Design and Analysis of Experiments. 5th ed. Wiley, New York, 696 pp.

Müller-Rutz J (1920) Aus der Welt der Kleinschmetterlinge mit Beschreibungen neuer Arten und Formen. Mitteilungen der Entomologia Zürich und Umgebung 5: 334–349, pl. 2.

Mutanen M, Aarvik L, Huemer P, Kaila L, Karsholt O, Tuck K (2012a) DNA barcodes reveal that the widespread European tortricid moth *Phalonidia manniana* (Lepidoptera: Tortricidae) is a mixture of two species. Zootaxa 3262: 1–21.

Mutanen M, Aarvik L, Landry J-F, Segerer A, Karsholt O (2012b) *Epinotia cinereana* (Haworth, 1811) bona sp., a Holarctic tortricid distinct from *E. nisella* (Clerck, 1759) (Lepidoptera: Tortricidae: Eucosmini) as evidenced by DNA barcodes, morphology and life history. Zootaxa 3318: 1–25.

Mutanen M, Hausmann A, Hebert PDN, Landry J-F, de Waard J, Huemer P (2012c) Allopatry as a Gordian knot for taxonomists: patterns of DNA barcode divergence in arctic-alpine Lepidoptera. PLoS ONE 7: e47214. doi: 10.1371/journal.pone.0047214

Mutanen M, Kaila L, Tabell J (2013) Wide-ranging barcoding aids discovery of one-third increase of species richness in presumably well-investigated moths. Scientific Reports 3: 2901. doi: 10.1038/srep02901

Ratnasingham S, Hebert PDN (2007) BOLD: The Barcode of Life Data System (http://www.barcodinglife.org). Molecular Ecology Notes 7: 355–364. doi: 10.1111/j.1471-8286.2007.01678.x

Robinson GS (1976) The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. Entomologist´s Gazette 27: 127–132.

Rougerie R, Kitching IJ, Haxaire J, Miller SE, Hausmann A, Hebert PDN (2014) Australian Sphingidae – DNA barcodes challenge current species boundaries and distributions. PLoS ONE 9(7): e101108. doi: 10.1371/journal.pone.0101108

Sinev SY (2008) Catalogue of the Lepidoptera of Russia. KMK Press, St. Petersburg-Moscow, 425 pp.

Svenson GJ, Whiting MF (2004) Phylogeny of Mantodea based on molecular data: evolution of a charismatic predator. Systematic Entomology 29: 359–370. doi: 10.1111/j.0307-6970.2004.00240.x

SwissLepTeam (2010) Die Schmetterlinge (Lepidoptera) der Schweiz. Eine kommentierte, systematisch-faunistische Liste. Fauna Helvetica 25, 349 pp.

Tamura K, Peterson D, Peterson N, Stechrer G, Nei M, Kumar S (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance and maximum parsimony methods. Molecular Biology and Evolution 28: 2731–2739. doi: 10.1093/molbev/msr121

Triberti P (2007) The *Phyllonorycter* species from Palaearctic region feeding on Rosaceae (Lepidoptera, Gracillariidae). Bollettino del Museo Civico di Storia Naturale di Verona. Botanica Zoologia 31: 147–221.

Wocke MF (1862) Reise nach Finmarken von Dr. Staudinger und Dr. Wocke. II. Microlepidoptera. Stettiner Entomologische Zeitung 23: 30–78, 233–257.

Zeller PC (1847) Die Gracilarien. Linnaea Entomologica 2: 303–383, 585–586, pl. II.

Zeller PC (1850) Verzeichniss der von Herrn Jos. Mann beobachteten Toscanischen Microlepidoptera (Schluss). Stettiner Entomologische Zeitung 11: 195–212.

Zetterstedt JW (1839) Insecta Lapponica. Lipsiae, 1140 pp.

Supplementary material 1

List of studied specimens of *Callisto coffeella* and *C. basistrigella* and collection data

Authors: Natalia Kirichenko, Peter Huemer, Helmut Deutsch, Paolo Triberti, Rodolphe Rougerie, Carlos Lopez-Vaamonde

Data type: collection data / voucher depository / genetic code.

Explanation note: The list of 135 examined specimens of *Callisto coffeella* and *C. basistrigella* sp. n., their collection data (country, locality, GPS coordinates, collection date and collector name) and depository data (museum or private collection) are provided in the supplementary table S1. All specimens have been studied morphologically; the barcoded samples are supplied with sample ID, process ID, GenBank COI and GenBank H3 (if nuclear gene histone H3 was analyzed).