

Doctoral Dissertation (Shinshu University)

Systematic revision of the Plectopylidae
(Gastropoda: Pulmonata)

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Abstract

Plectopylidae is a land snail family which belongs to the order Stylommatophora, and distributed in large part of East Asia from Nepal to Okinawa. Most of the approximately 100 known species were described at the end of the 19th, and the beginning of the 20th centuries. Since then, nearly no publications were dealing with the family. I revised every taxa of the Plectopylidae based on type, non-type, and newly-collected materials. During the taxonomic revision I was focusing on the morphological characters of the shells, the reproductive anatomy and the radula. The revision resulted in the description of two new subfamilies, two new tribes, seven genera and subgenera, 32 species and subspecies. Twenty-six taxa are turned out to be synonyms. Approximately half of the known, valid taxa had to be moved to other genera. I also investigated some of the living and fossil land snail groups which were assigned to the family Plectopylidae by earlier taxonomic works. In two cases (genera *Zilchistrophia* and *Amphicoelina*) my data suggest that they do not belong to the Plectopylidae, but are the members of other families, namely Scolodontidae and Camaenidae, respectively. I confirmed the taxonomic position of the Chinese Eocene genus *Plectopyloides* inside the Plectopylidae. The other, European and Indian Cretaceous fossil groups which were previously assigned to the Plectopylidae, are probably not related to this family. The investigation of the anatomy of the Plectopylidae resulted in two main conclusions: (1) an organ of previously unknown homology proved to be a diverticulum, and (2) the presence of disposable, usually hook-like calcareous granules inside the penis suggest that they are probably used during mating season only. This is the only known case of mating disposable hook-like structures inside the male reproductive organs of land snails.

Chapter1: Introduction

What is taxonomy and systematics?

Systematics is a discipline which describes, classifies and names organisms, provides identification keys, investigates the evolutionary histories and their environmental adaptations (Michener et al. 1970). Systematics, systematic biology, biological classification and taxonomy are terms that are often used interchangeably. For sake of simplicity, I do not distinguish these terms from each other and use them as synonyms for morphology-based classification of organisms.

What kind of discipline is taxonomy?

Taxonomy deals with hypothesis testing on multiple levels. Every Linnaean rank is a hypothesis. The claim that two structures are homologous is also a hypothesis (Wheeler 2004). Taxonomy is usually not recognized as an experimental discipline. Contrary to this view, the procedure of hypothesis testing (=experiment) is part of taxonomic studies.

What are the logical steps in taxonomy?

In experimental disciplines, the scientific result is the outcome of an experiment. An experiment is a procedure to verify, refute, or establish the validity of a hypothesis. A hypothesis is a proposed explanation for a phenomenon. Hypotheses are scientific when they are testable (refutable). Phenomena are any observable occurrences, in other words, primarily observations or data.

In taxonomy, data are the observable morphological features. Taxonomists observe the combination of characters and their attributes of being discrete or continuous across specimens and samples. Based on primarily observations, taxonomists propose hypotheses. For example, an observation is when we see two similar structures in similar relative position in the body of two organisms. We can hypothesize that they are homologous, which means that they share common ancestry. It is possible to focus on these hypothesis and try to test them, but making a step further (=compare homologous structures in order to propose taxa hypotheses) does not require the verification of supposed homologies. In this case the hypothesis on the homology remains a so-called working hypothesis. Using the working hypothesis of homologous structures we can make comparisons and we can propose taxa hypothesis based on the unique combinations of characters and the gaps in the morphological continuum. A taxon, for example a genus is hypothesis, namely a proposed explanation why certain organisms share similar homologous structures. The explanation for *why* is that they share a common ancestor. These taxa hypotheses are testable using for example sequence data of biological macromolecules. Observation of previously not examined or insufficiently examined specimens may reveal that the combination of characters differ from the hitherto recognized combinations. Both approaches mentioned can be useful to refute or support a taxon hypothesis.

What is the taxonomic impediment?

Increasing mass of data suggests that taxonomy is in a crisis. Taxonomy has an overall negative reputation among experimental biologists. This negative reputation together with other factors results in fewer academic positions in taxonomy, fewer grants, etc., and makes morphology-based taxonomic research difficult. The difficulties taxonomy is and taxonomists are facing are often quoted as parts of the "taxonomic impediment" (Wheeler et al. 2004, de Carvalho et al. 2005, 2007, Evenhuis 2007, Padial & De la Riva, 2007, Venu & Sanjappa 2011, Ebach et al. 2011). In this chapter I list some component of the taxonomic impediment.

(1) Gap between primarily observations and results:

The results and discussion of an experimental study should be in a healthy balance with the material used and methods applied. Classic taxonomy on the other hand, uses observations of morphological data, and proposes Linnaean ranks which are hypothesis of evolutionary history. The most powerful method to reveal the evolutionary relationships is molecular phylogeny. Since phylogeny became a routine tool, morphology-based hypotheses on evolutionary history became neglected. The most influential species concepts (biological s.c.: Mayr 1942, phylogenetic s.c.: Eldredge & Cracraft 1980, cohesion s.c.: Templeton 1989, genic s.c.: Wu 2001, general lineage s.c.: de Queiroz 1998, differential fitness s.c.: Hausdorf 2011) do not even mention morphology. Some researchers outside of taxonomy may believe that the morphological information is simply not enough to hypothesize what a species is and what is not. This belief results in an overall negative reputation of morphology-based research.

Proposing and revising Linnaean ranks are often quoted as taxonomic decisions among taxonomists. The word *decision* indeed describes the nature of taxonomy well. Taxonomists often have to make decisions, even if the

available information is seemingly insufficient. Furthermore, there is an increasing gap between phylogeny and taxonomy. The results of phylogenetic studies are rarely transformed into revisions of Linnaean names (Franz 2005). This indicates that many researchers working on phylogenetic trees are not interested in classification.

(2) Linnaean ranks do not exist:

Phyla are often defined by the unique body plan (Erwin et al. 1997, McHugh 1997), and we can find several paper which try to define the rank genus (Edwards 1953, Allmon 1992, Wood & Collard 1999). Linnaean ranks between the genus and the phylum are possibly never defined in the literature. There is a never ending argument even about the reality of species, which is probably the most important terms in supraindividual biology (Coyne & Orr 2004). The lowest rank used in animal taxonomy, and accepted by the ICZN Code (Ride et al. 1999) is subspecies. The necessity and usefulness of subspecies have been questioned and criticized from time to time (Frost & Hillis 1990, Burbrink et al. 2000, Manier 2004). Subspecies have largely been neglected in species concepts other than the biological species concept (Mayr 1942) because the main difference between species and subspecies is reproductive isolation. Under popular, recently introduced species concepts, such as the general lineage (unified) concept (de Queiroz 2005a,b), subspecies do not make sense. As a result, several former subspecies were elevated to species level. This phenomenon is described as taxonomic inflation (Isaac et al 2004, Harris & Froufe 2005, Knapp et al 2005, Mallet et al. 2005) and calls the attention of the importance of maintaining a rank below species. In face of the usual rejection of subspecies by most evolutionists, hundreds of new subspecies are described every year, sometimes even with molecular information and strong theoretical support (e.g. Hawlitschek et al 2012). Some others authors, mainly the ones who deal with vertebrates, often argue for subspecies. For instance, subspecies are found to be useful in conservation (Phillimore & Owens 2006), and for identifying distinct populations within biological species (Remsen 2010). Subspecies are evaluated as being convenient for managing taxonomical entities (Fitzpatrick 2010).

In face of the debates regarding the practical usefulness of some Linnaean ranks and the lack of definition of most absolute categories, rank-based nomenclature is still the most wide-spread framework to categorize organisms in light of their assumed evolutionary relationships. Alternative (non-Linnaean) taxonomic methods, such as the phylogenetic nomenclature (De Queiroz & Gauthier 1990, 1992, Laurin, 2010), are not yet widely used in biology and in morphology-based taxonomy it is not used at all. In Linnaean taxonomy, ranking decisions are influenced by previous generations of taxonomists. These ranking traditions are highly variable between taxa since taxonomists often specialize in one or a few closely related taxa, and communication between specialists of different clades happens very rarely. For such reasons, ranking taxa into Linnaean categories is almost universally recognized as a fairly subjective action among taxonomists (Laurin, 2010). This, in combination with the taxonomic species concept ("whatever a competent taxonomist chooses to call a species", Blackwelder 1967), suggests that taxonomy is nothing more but subjective grouping of organisms.

(3) Too much bad taxonomy:

Describing a species is relatively easy, because many (most?) taxonomic journals lack a peer-reviewed policy. In Europe, 60 % of new species have been described by non-professionals (Fontaine et al. 2012). Thus, amateurs form an essential part of the workforce in taxonomy, and many of them are doing invaluable research. On the other hand, several amateur taxonomists do not have the background in biology. This combined with the overall poor review process results in low quality publications throughout the whole discipline. Another large, and yet unsolved problem is that the ICZN Code (Ride et al. 1999) allows to publish new taxonomic names practically in any languages of the world. The above listed problems are intrinsic difficulties of taxonomy which must be solved by the community of taxonomists.

(4) Evaluation of taxonomists

Citation-based evaluations, such as Impact Factor and number of citations cannot be fairly used in taxonomy (Valdecasas et al. 2000). During evaluation by citation-based methods, taxonomists have no chance to compete with researchers of other disciplines, such as ecology and molecular biology. Generally low IF of taxonomists is partly resulted by the low citation rates of taxonomic papers. The reason behind is that the number of taxonomists is declining; taxonomy does not follow the exponential curve of most sciences. The average age of references in taxonomic publications is much greater than those in other scientific disciplines. Krell (2002) analysed 2,091 references from seven randomly chosen taxonomic papers and found that 98.5 % of the references were more than two years old. As a consequence, papers cited more than two years after their publications do not count for IF. Moreover, for any group of organisms there are at best a handful of (or frequently no) extant specialists. Therefore

the chance to become cited by colleagues is relatively rare compared with other fields (Krell 2002). The second reason for the low impact factor in taxonomy is the low percentage of journals which are scanned by the Institute of Scientific Information (ISI). Approximately 93 % of potentially relevant journals are not considered. It is good luck rather than a sign of good quality to be included in the ISI (Krell 2000). A third reason for the low IF can be the fact that the relevance of descriptive publications in this field remains the same over time; original descriptions have to be referred to for ever, independent of the paper's quality. Outside taxonomy, however, referring to original descriptions becomes superfluous with time and/or revisions (Valdecasas et al. 2000, Venu & Sanjappa 2011). The original descriptions of model organisms, invasive species and prominent species such as the Komodo dragon, are usually not cited. This obsolescence underestimates impact for authors of well-studied species (Köhler 1988, Wägele et al. 2011). A fourth reason may be that identification keys used during a study to identify organisms are also usually also not documented in reference lists (Krell 2002).

To find a solution for more fair evaluations of taxonomic publications, Valdecasas (2011) introduced the T-Index, which is a formula which results in the highest number when all taxa of a given clade are included in the publication. Some minor corrections of the T-Index has been proposed and accepted (Páll-Gergely 2014, Valdecasas 2014).

The recently introduced M-Index (Pyke 2014) is a citation-based index which uses not the cited publications listed in the references, but computer software to search for mentions of particular scientific names. The M-Index can indeed be useful for a small number of taxonomic publications, especially because we cannot reasonably expect non-taxonomists to cite original descriptions. However, the way Pyke (2014) introduced the M-Index as a tool for evaluating the quality of taxonomic publications is a misinterpretation of the connection between the quality and the impact of a publication; a phenomenon which has been discussed in a number of publications (e.g. Krell 2000, Ebach et al. 2011). For example, the horse-chestnut leaf miner (*Cameraria ohridella* Deschka & Dimic, 1986) has not been cited more than a thousand times (Wägele et al. 2011) because of the excellent quality of the original description, but the fact that it became an invasive species in large part of Europe (Sefrova & Lastuvka 2001). The same is true for the popular model species, *Caenorhabditis elegans* (Maupas 1899), which received ca. 173,000 Google Scholar hits (Wägele et al. 2011) regardless of the quality of its original publication. Similarly, the reason why thousands of tiny Tropical invertebrate species has never been mentioned since their descriptions is not because of the low quality of their original descriptions. The widespread misconception in scientific metrics, namely that quality is the same as impact, has an overall very negative effect on taxonomists (Páll-Gergely 2015).

(5) Decline of the number of taxonomists and taxonomic activity

Currently there are few sources for funding taxonomic revisions or training taxonomists. Money for taxonomy is channelled into projects such as DNA barcoding. As a result, many of those who used to work taxonomic groups from morphological approach today do so at the molecular level. Additionally, fewer and fewer students consider taxonomy as a career prospect (Ebach et al. 2011).

(6) End-user mentality:

It seems several authors look at taxonomy as identification service for evolutionary and conservation biology and ecology. Costello et al. (2013b) narrowly defined taxonomists as the people describing species new to science. De Carvalho et al. (2014) claimed that this is akin to defining racing car drivers as those who own a car. Similar view to that of Costello et al. (2013b) is shared by other recent authors, such as Godfray (2007), Miller (2007), Joppa et al. (2011) and Scheffers et al. (2012). These papers, all published in high ranked journals diminish the resources needed for the proper education and employment of taxonomic specialists (de Carvalho & Ebach 2010), and do not recognize taxonomy as an independent discipline which plays a crucial role in understanding the diversity of life.

Contradicting opinions on the taxonomic impediment

Some recent papers (e.g. Joppa et al. 2011, Costello et al. 2012, 2013a) argue that the number of taxonomists and taxonomic effort is increasing. In face of this, fewer new species are described now, than when less taxonomists were active. According to their explanation, this is the indication of the increasing difficulty to find new species, and that taxonomic research is not in a crisis.

Bebber et al. (2014) was arguing for the contrary. They showed that compared to other scientific disciplines the increased number of authors (=author inflation) on taxonomic papers is relatively small and may reflect changes in scientific practice rather than an increase in taxonomic effort. Students, collectors, technicians, and others, who are involved in one stage of species discovery, are credited more than before. Additionally, there is an average lag period of 35 years between a specimen being collected and published as a new species. The data of Bebber et al. (2014)

suggest that the taxonomic capacity to describe new species of flowering plant is stagnant. This suggests that the pool of unknown species does not seem to become recognisably smaller yet.

Why is morphology-based taxonomy important?

The importance of morphology-based taxonomic research can be interpreted by two approaches: First, the outcome of the taxonomic work itself, in order to satisfy human curiosity, and second, the application of taxonomic information by to other disciplines.

May (2010) noted that the first question a visiting alien species might ask us is, "How many distinct life forms (species) does your planet have"? Knowing how many species inhabits the earth has always been one of the most important questions in biology. A recent study estimated 8.7 million 6 ± 1.3 million eukaryotic species globally, of which approximately only 1.2 million has already been described (Mora et al. 2011). With the current tendency (ca. 16,000 species/year) this will take 1,200 years. Every taxonomic revision is a little step to answer this simple-looking question.

Besides curiosity, detailed knowledge on the earth's biodiversity helps us to identify biodiversity hotspots (Myers et al. 2000) and protect our species more effectively in order to maintain ecosystem services for human wellbeing (Balvanera et al. 2006). Detailed morphological, behavioural, ecological, distributional information which are the outcome of taxonomic research provokes further questions in evolutionary biology, ecology, ethology, etc. Morphology often allows field biologists to observe plants and animals in the field quickly and without destructive sampling. Morphological characters are the only bridge between fossil and recent species. Morphological characters are frequently the object of natural selection (Wheeler 2008).

What happens when we neglect taxonomic research and correct identifications?

It is difficult to add a satisfactory answer to this question, because taxonomic information is used by nearly all disciplines at least in supraindividual biology. Some signs of neglecting correct identifications already undermines the reliability of databases such as the GenBank. For example, up to 20% of GenBank entries of Fungi are incorrectly identified on species level (Nilsson et al. 2006). Some examples are known when authors drew conclusions on the evolutionary history of certain organisms based on DNA sequences of obviously misidentified specimens (Steinke et al. 2004, Groenenberg et al. 2011). To elevate the reliability of the identifications of sequence data is very important challenge of in the 21st Century. Sequence information only provides information when the organism it belongs to is correctly identified. The correct name is not just a label on a museum sample, but a shorthand notation of for a hypothesis regarding the distribution of attributes among populations (Nixon & Wheeler 1992b).

About molluscs and snails in general

Molluscs (phylum Mollusca) represent the second largest phylum after arthropods. The described species of molluscs vary from ca. 50,000 (Tangley 1997, Bouchet 2006) to 120,000 (Ponder et al. 2002). Chapman (2009) referred to personal communication with G. Rosenberg (Sept. 2008), who estimated 200,000 mollusc species worldwide. Bouchet et al. (2005) estimate 60,000–80,000 species of snail (Gastropoda) species which are classified into 409 families. Additional 202 families appear only in the fossil record. All terrestrial molluscs belong to the class Gastropoda (snails). Lydeard et al. (2004) estimated 24,000 terrestrial species of molluscs. Terrestrial molluscs do not form a monophyletic unit. Most species belong to the clade Stylommatophora of the order Pulmonata, which includes air-breathing terrestrial snails and slugs. The minority of terrestrial snail species belong to the clade Caenogastropoda. Stylommatophoran gastropods lack, but caenogastropods possess an operculum, which is a door-like structure which closes the aperture when the snail withdraws itself to the shell.

Southeast Asian malacology

Large areas of the Southeast Asian Region, such as South-Central China, Indo-Burma, Sundaland and Philippines are considered as biodiversity hotspots (Myers et al. 2000). After arthropods, molluscs represent the second largest phylum in terms of number of known species. Discoveries of land snail species in the region were most intensive at the end of the 19th and the beginning of the 20th Centuries. For example, in Vietnam, 77% of all known Stylommatophoran snails were described between 1880 and 1920. Since then, nearly no taxonomic groups were studied intensively in that country. One exception is the family Clausiliidae. The several recently described clausiliid species (Maassen & Gittenberger 2007, Nordsieck 2011, Grego et al. 2014) indicates that the low number of recently described species in other groups is not because no species left unknown after the activity of naturalists at the end of the 19th Century.

Since the early 20th Century only few papers reported new species from countries such as China, Vietnam, Myanmar and Nepal. Moreover, most of the species were described on the basis of few empty shells. The soft anatomy, which plays a crucial role in their classification, is known in a few species only. Our pre-existing knowledge on their distribution is also scarce due to the lack of exact localities in the literature and on labels of museum lots. Consequently, the number of undescribed species might be very large, and the systematic position and distribution of described species is uncertain or unknown in many cases. Recent revisionary works focusing on Southeast Asian snails are rare, while the necessity of detailed taxonomical and distributional data during the 6th mass extinction is growing (Dirzo & Raven 2003, La Salle et al. 2009).

Why Plectopylidae?

The family Plectopylidae is a group of Asian pulmonate land snails. It is a typical family of that region because it has been studied most intensively ca. a century ago. The approximately 100 known plectopylid species and the many new species which was awaiting discovery offered ideal conditions to perform a revision of the family for a PhD thesis during a three years period. Additionally, the family Plectopylidae is unique in the proportion of sinistral and dextral genera compared with other flat and globular shelled groups. Based on Zilch (1959–1960), Asami et al. (1998) reported that there are 457 flat or globular shelled stylommatophoran genera which contain only dextral species, 8 genera contain only sinistral species, whereas two genera are known to include sinistral and dextral species as well. This means that the vast majority of flat or globular shelled stylommatophoran gastropods are dextral, and only 2.1 % of the genera contain sinistral species. In contrast, this ratio is 33.6 % in high-spired genera. In the family Plectopylidae, however, there are two dextral and two sinistral genera, and one genus contains both sinistral and dextral species (Gude 1899e; *Enteroplax* and *Ruthvenia* were not counted). This makes the proportion of sinistral and mixed genera 60 % in the Plectopylidae, which is extremely high compared with the ca. 2 % in all flat shelled genera. To understand the background of this outstandingly high ratio of sinistral and mixed genera, we need strong taxonomical basis.

My thesis presents the taxonomic revision of the land snail family Plectopylidae based on the examination of all available type specimens, non-type museum material, and newly examined specimens. Shell, anatomical and radula characters were examined in order to define taxa (subfamilies, tribes, general, subgenera, species and subspecies) within Plectopylidae.

Chapter 2: Material and Methods

Material

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 old 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, shell plates, armature drawings and species remarks.

I visited the following public institutes:

Hungarian Natural History Museum Budapest (Hungary)
Natural History Museum, Sibiu (Romania)
The Natural History Museum, London (United Kingdom)
Naturhistorisches Museum Wien (Vienna, Austria)
Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main (Germany)
Paleontological Museum Munich (Germany)

I received specimens or photos from the following public institutions and private collectors:

Academy of Natural Sciences (Philadelphia, USA)
András Hunyadi (Budapest, Hungary)
Hao Yang (China)
Hiroshi Minato (Shirahama, Japan)
Jamen Uiriamu Otani (Osaka, Japan)
János Podani (Budapest, Hungary)
Jens and Christa Hemmen (Wiesbaden, Germany)
Jozef Grego (Banská Bystrica, Slovakia)
Kenji Ohara, Nishinomiya Shell Museum (Nishinomiya, Japan)
Miu Yeung (Hong Kong, China)
Museum of Comparative Zoology (Massachusetts, USA)
Museum für Naturkunde (Berlin, Germany)
Muséum National d'Histoire Naturelle (Paris, France)
Paratype collection of the Nishinomiya Shell Museum
Royal Belgian Institute of Natural Sciences (Brussels, Belgium)
Senckenberg Museum für Naturkunde Görlitz (Görlitz, Germany)
Smithsonian National Museum of Natural History (Washington, USA)
Statens Naturhistoriske Museum (Copenhagen, Denmark)
András Varga (Gyöngyöshalász, Hungary)
Wim J. M. Maassen (Echt, The Netherlands)
Yifan Zhao (China)
Zoltán Péter Eröss (Budapest, Hungary)
Zoological Museum, Hamburg (Germany)

Localities

The Chinese geographic names are presented in pinyin without tone numbers. Only names of populated places (district=Xian, town region=Shi, community=Xiang and Zhen, Cun= village and autonomous regions=Zizhizhou, Zizhixian, Zizhiqu) are written separately. Geographic names, such as mountain (shan), cave (dong) rock (yan) forest (lin) are not written separately. The Appendix includes all mentioned Chinese localities and their respective provinces presented in simplified Chinese characters. The exact descriptions of locations are given from province to village. Only exact locations of newly collected material are designated on maps (except Map 1.). Species with unknown or uncertain locality data are presented on Map 2.

All Vietnamese localities mentioned in the literature are shown on Figure 7.109. The distances between parapatric populations which were collected closer than 10 km were measured using Google Earth (Tables 2.1–2.4).

All localities of Genus1, *Chersaecia*, *Endoplon*, *Endothyrella* and *Plectopylis* taxa mentioned in the literature and on museum labels are compiled in Table 7.10.

Images

Photographs of several focal planes were made with a “Wild Makroskop M420” and a “Nikon DS Camera Control Unit DS-L2”. The different layers were combined with “Helicon Focus 4.75 Pro” to obtain one completely focused image.

The photo of the internal genital morphology was taken via a Zeiss Discovery V20 Microscope, Plan-Apo S objective, 0.63, Zeiss AxioCam HRc camera and use of the Axio Vision 4.8 programme.

Shells were directly observed without coating under a low vacuum SEM (Miniscope TM-1000, Hitachi High-Technologies, Tokyo).

The buccal mass was removed and soaked in 2 molar KOH solution for 5 hours before extracting 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).

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, I used the terms "distal" and "proximal" in relation to the genital atrium. At dissection of each specimen, I recorded whether embryos are present in the uterus and calcareous granules on the internal surface of penis (Table 7.1). I used Fisher's exact test 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 7.2–7.3).

Morphological characters

I examined the following traits of the shell, the reproductive anatomy and the radula.

Shell characters:

- (1) Direction of the coiling: sinistral or dextral
- (2) Colour of the shell, presence/absence of a band around the umbilicus
- (3) Shell size
- (4) Height of the spire; this trait is connected to the depth/width of the umbilicus
- (5) Shape of the whorls from dorsal view (bulging or flat); this trait is connected to the depth or the suture.
- (6) Shape of the whorls from apertural view: rounded, keeled, shouldered
- (7) Number of protoconch and teleoconch whorls
- (8) Sculpture of the protoconch: The protoconch is the part of shell which has been developed during the embryonic stage, before hatching. The boundary between the embryonic whorls and the postembryonic whorls is visible in all non-corroded shells. The fine sculpture (surface) of the protoconch is probably not an adaptive character, therefore it is useful for taxonomic categorization.
- (9) Sculpture of the teleoconch: dorsal, ventral surfaces; the position of their transition on the body whorl
- (10) Presence/absence/morphology of periostracal folds (hairs)
- (11) Shape of the aperture
- (12) Morphology of the peristome: how much thickened, and how much reflexed
- (13) Shape, height and sharpness of the parietal callus
- (14) Presence/absence of the apertural fold; if present, connected to the callus/free from the callus
- (15) Morphology of the palatal plicae
- (16) Morphology of the parietal plicae and lamellae

Anatomical characters:

- (1) Presence/absence of an additional organ next to the atrium
- (2) Position of the ommatophoral retractor which corresponds to the coiling direction
- (3) Outer morphology of the penis
- (4) Morphology of the inner wall of the penis
- (5) Morphology of the calcareous granules inside the penis
- (6) Presence/absence of the epiphallus and its outer morphology
- (7) Morphology of the inner wall of the penis epiphallus
- (8) Morphology of the vas deference

- (9) Presence/absence/morphology of the penial caecum
- (10) Presence/absence/morphology of the retractor muscle
- (11) Morphology of the vagina
- (12) Presence/absence/morphology of the diverticulum
- (13) Morphology of the bursa copulatrix

Radula characters:

- (1) Number of laterals and marginals
- (2) Size of the central tooth compared to the ectocones of the first laterals
- (3) Morphology of the mesocone of the laterals
- (4) Morphology of the marginals: number of cusps, their sharpness and the depth of the incision between the cusps

Taxonomic treatment

The taxonomic revision is based on morphology by examination of specimens and literature. All taxa are defined based on unique combinations of morphological traits. Some of the characters are discrete in nature (e.g. presence or absence of periostracal filaments) or continuous but with distinct gaps (e.g. shape of the callus).

The present morphospecies 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 groups. Tables 2.1–2.4 show sympatric species pairs. I found no specimens that show transitional characters between sympatric species. This suggests that these are biological species reproductively isolated from each other.

Generally, the shell and aperture shape was primarily important in recognizing allopatric species. In some cases I have not found differences in the shell and aperture shapes of allopatric populations, but I found stable differences in the armatures. In those cases I handled them as different species and subspecies.

Major differences in the plication resulted in differentiation on species level:

- (1) presence/absence of the anterior lamella (*Chersaecia goniobathmos* and *Ch. refuga*; *Gudeodiscus yunnanensis* and *G. cyrtochilus*)
- (2) presence/absence of a long lower parietal plica (*Gudeodiscus dautzenbergi* and *G. villedaryi*)
- (3) presence/absence of the lower and main plicae (*Chersaecia shanensis* and *Ch. species1*; *Endothyrella blanda* and *E. williamsoni*)
- (4) Horizontal or oblique palatal plicae (*Sicradiscus invius*, *S. feheri*)

Minor differences in the plication resulted in differentiation on subspecies level:

- (1) differences in shell sculpture (*Gudeodiscus eroessi eroessi* and *G. eroessi hemisculptus*; *Endothyrella plectostoma plectostoma*, *Endothyrella plectostoma exerta* and *Endothyrella plectostoma tricarinata*, *Gudeodiscus emigrans* spp.)
- (2) differences in spire height (*Gudeodiscus pulvinaris pulvinaris* and *Gudeodiscus pulvinaris robustus*; *Gudeodiscus eroessi* spp.; *Gudeodiscus giardi* spp.)
- (3) differences in the palatal plicae (*Endothyrella macromphalus macromphalus* and *Endothyrella macromphalus gregorsoni*; *Gudeodiscus emigrans* spp.)
- (4) apertural fold connected to the callus or free from it (*Gudeodiscus giardi* spp.)
- (5) differences in the strength of the callus (*Gudeodiscus pulvinaris pulvinaris* and *Gudeodiscus pulvinaris robustus*; *Gudeodiscus eroessi eroessi* and *Gudeodiscus eroessi fuscus*; *Sinicola reserata* spp.)
- (6) presence/absence of the main plica (*Chersaecia refuga* and *Ch. refuga muspratti*; *Chersaecia perarcta perarcta* and *Ch. perarcta simplex*)
- (7) presence/absence of the intermediate plica (*Chersaecia shiroiensis* and *Ch. shiroiensis* subspecies1)
- (8) lower plica exceeds of the anterior lamella or not (*Gudeodiscus messengeri* and *Gudeodiscus messengeri raheemi*)
- (9) presence or absence of two long horizontal plica between the upper and lower parietal plicae (*Sinicola reserata* spp.)

Synonyms

Previously recognized taxa were synonymized when their differences between other species (often present as only a few individuals) can be interpreted as intraspecific diversity.

Abbreviations:

ACNMW: Amgueddfa Cymru - National Museum Wales (Cardiff, UK)
 ANSP: Academy of Natural Sciences (Philadelphia, USA)
 EZP: Collection Zoltán Péter Eröss (Budapest, Hungary)
 HA: Collection András Hunyadi (Budapest, Hungary)
 HNHM: Hungarian Natural History Museum (Budapest, Hungary)
 JG: Collection Jozef Grego (Banská Bystrica, Slovakia)
 JH: Collection Jens and Christa Hemmen (Wiesbaden, Germany)
 JUO: Collection Jamen Uiriamu Otani (Osaka, Japan)
 MCZ: Museum of Comparative Zoology (Massachusetts, USA)
 NHMSB: Natural History Museum, Sibiu (Romania), Bielz collection
 NHMSK: Natural History Museum, Sibiu (Romania), Kimakowicz collection
 NHMUK: The Natural History Museum (London, UK)
 NHMUKw: The Natural History Museum, spirit collection (London, UK)
 MNB: Museum für Naturkunde (Berlin, Germany)
 MNHN: Muséum National d'Histoire Naturelle (Paris, France)
 NCP: Paratype collection of the Nishinomiya Shell Museum
 NHMW: Naturhistorisches Museum Wien (Vienna, Austria)
 OK: Collection Kenji Ohara, Nishinomiya Shell Museum (Nishinomiya, Japan)
 PGB: Collection Barna Páll-Gergely (Mosonmagyaróvár, Hungary)
 PJ: Collection János Podani (Budapest, Hungary)
 PMM: Palaeontological Museum Munich
 RBINS: Royal Belgian Institute of Natural Sciences (Brussels, Belgium)
 SMF: Senckenberg Forschungsinstitut und Naturmuseum (Frankfurt am Main, Germany)
 SMNG: Senckenberg Museum für Naturkunde Görlitz (Görlitz, 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)
 ZMH: Zoological Museum, Hamburg (Germany)
 ZMUC: Zoological Museum, University of Copenhagen (Denmark)
 D: shell diameter
 H: shell height
 u. gen.: undescribed genus (genus which will be described after the PhD defence)
 u. sp.: undescribed species (species which will be described after the PhD defence)
 u. ssp.: undescribed subspecies (subspecies which will be described after the PhD defence)
 u. subfam.: undescribed subfamily (subfamily which will be described after the PhD defence)
 u. trib.: undescribed tribe (tribe which will be described after the PhD defence)
 s. l.: sensu lato (in a wider sense)
 s. s.: sensu stricto (in a stricter sense)
 Wh: whorl

Table 2.1. 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.

	<i>anceyi</i>	<i>fischeri</i>	<i>francoisi</i>	<i>giardi</i>	<i>phlyarius</i>	<i>hemmeni</i>	<i>mansuyi</i>
<i>cyrtochilus</i>							***
<i>dautzenbergi</i>					**		
<i>fischeri</i>	**						
<i>francoisi</i>	***						
<i>giardi</i>	***		***				***
<i>messengeri</i>					*		
<i>m. raheemi</i>					***	***	
<i>phlyarius</i>	***		**	**			**
<i>quadrilamellatus</i>	***	**					
<i>suprafilaris</i>	**		**	***	**		***
<i>villedaryi</i>	***				***		

Table 2.2. Co-occurrence of Plectopylidae inhabiting Guangxi and Yunnan Provinces. 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 (*feheri-yunnanensis*: 1050 m; *feheri-cyrtochilus*: 8760 m; *pulvinaris robustus-concavus*: 4760 m; *emigrans otanii-eroessi hemisculptus*: 540 m; *fimbriosa-multispira*: 4310 m).

	<i>feheri</i>	<i>concavus</i>	<i>e. otanii</i>	<i>phlyarius</i>	<i>eroessi</i>	<i>p. robustus</i>	<i>soosi</i>
<i>yunnanensis</i>	**						
<i>cyrtochilus</i>	**						
<i>p. robustus</i>		**			***		
<i>e. hemisculptus</i>			**	***			
<i>phlyarius</i>			**			***	
<i>okuboi</i>					***	***	
<i>transitus</i>						***	***

Table 2.3. Co-occurrence of Plectopylidae inhabiting Hunan, Hubei and Sichuan Provinces. 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 (*asamiana-invius*: 240 m; *fimbriosa-multispira*: 4310 m).

	<i>r.</i> <i>azona</i>	<i>stenochila</i>	<i>multispira</i>	<i>diptychia</i>	<i>invius</i>	<i>asamiana</i>
<i>schistoptychia</i>	***					
<i>diptychia</i>	***					
<i>jugatoria</i>	***		***			
<i>fimbriosa</i>		***	**	***		
<i>emoriens</i>			***			
<i>asamiana</i>					**	
<i>murata</i>					***	***

Table 2.4. Co-occurrence of *Endothyrella* species. Two stars indicate that the two species were collected at geographically close sites by the same or different collectors (species8-nomenovum1: 2680 m). One star indicates frequent presence of the two species mixed within museum samples.

	species8	<i>blanda</i>	<i>macromphalus</i>
nomenovum1	**		
<i>pinacis</i>		*	
<i>minor</i>		*	*
<i>blanda</i>			*

Chapter 3: Terminology

Counting of the whorls

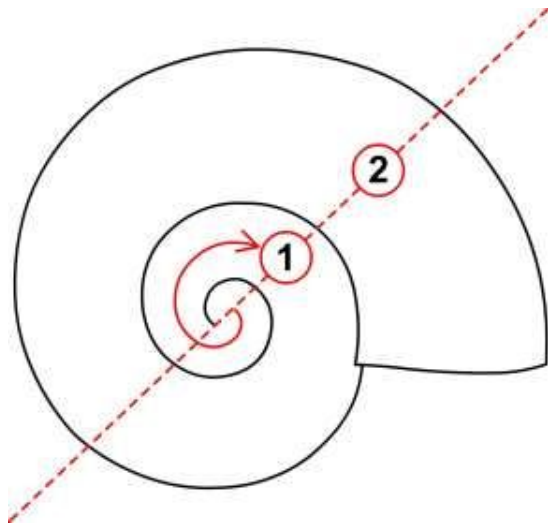


Figure 3.1. How to count the whorls (exactness 0.25) (after Kerney & Cameron 1979).

Shell size

The differences in size are indicated in the diagnosis with the following terms: tiny (smaller than 6 mm), very small (6–10 mm), small (10–15 mm), middle-sized (15–20 mm), large (20–25 mm), very large (25–30 mm).

General views of the shell and its parts

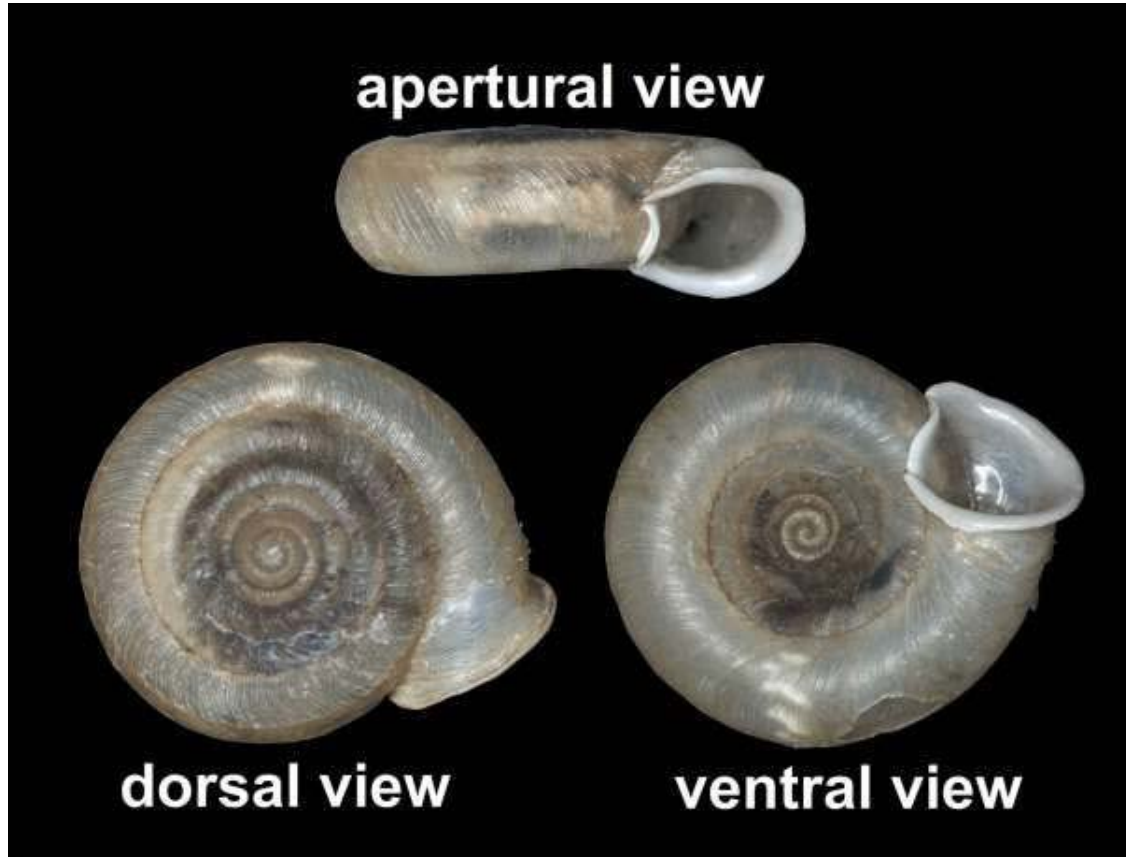


Figure 3.2. Three views of a plectopylid shell.

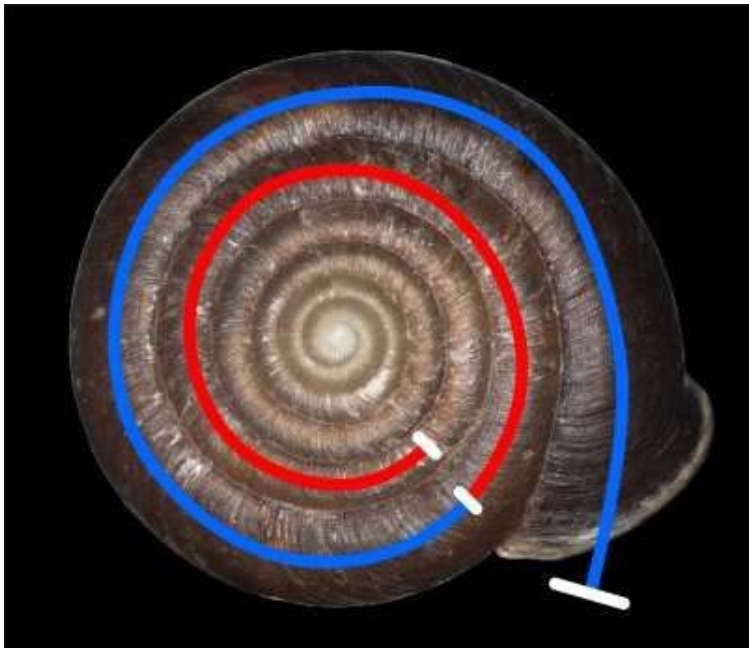


Figure 3.3. Definition of the whorls. The last whorl is indicated by blue, and the penultimate (preceding) whorl is indicated by red.

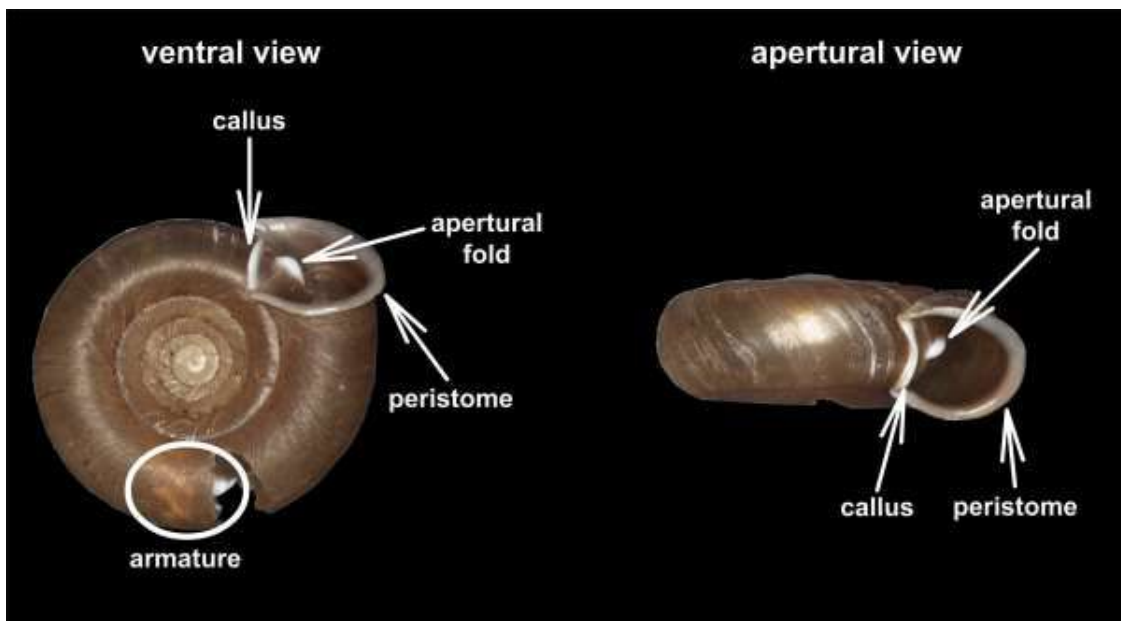


Figure 3.4. Names and locations of apertural structures and armature inside the last whorl.

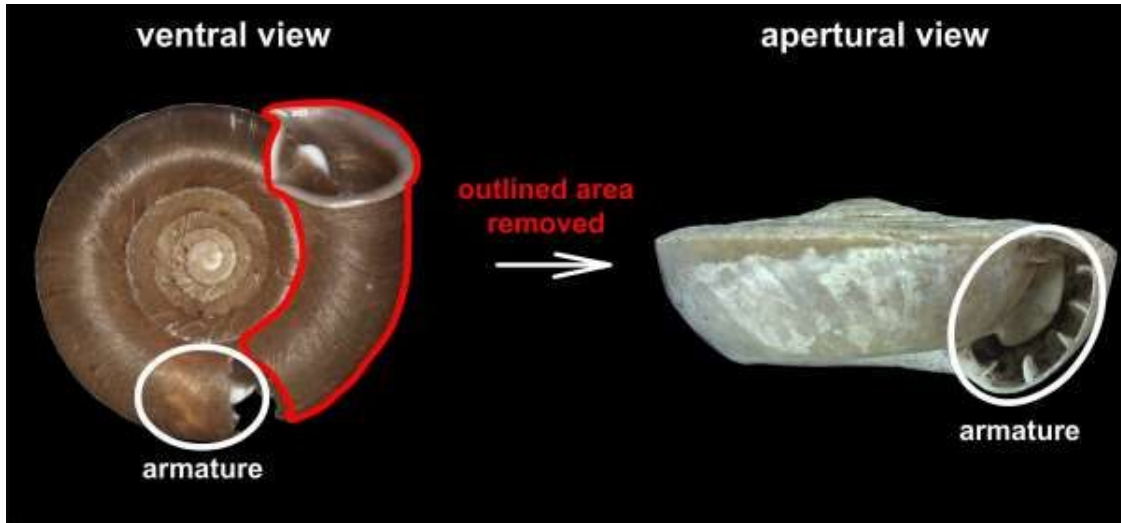


Figure 3.5. How to expose the structure of armature in apertural view.

Position and nomenclature of the plication

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 visible through the shell wall (external view).

As far as I could see, the juvenile armatures are very similar to the last, final one in adult specimens. Hence, in most cases, these can also be used for identification. In this thesis however, only the last ultimate armature is shown, which is situated about one quarter/half whorl behind the developed adult apertural lip.

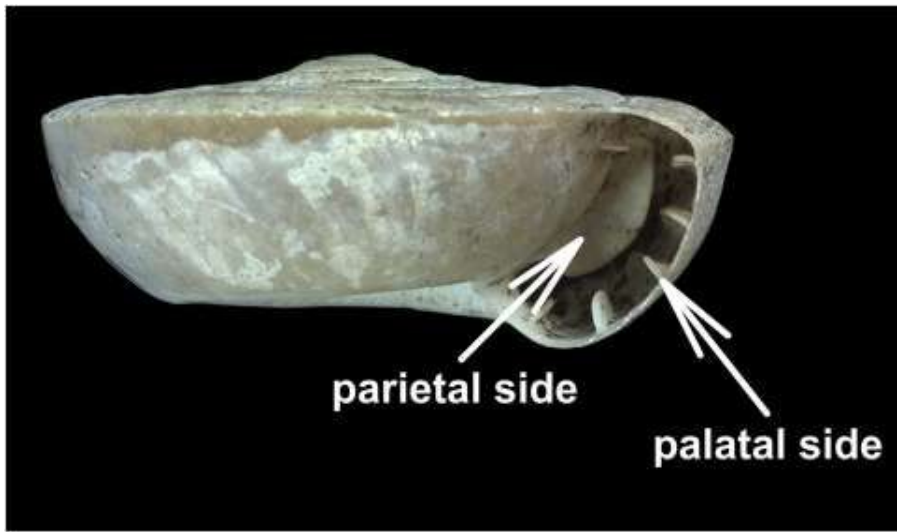


Figure 3.6. Definitions of parietal and palatal sides of the armature on the internal surface of last whorl.

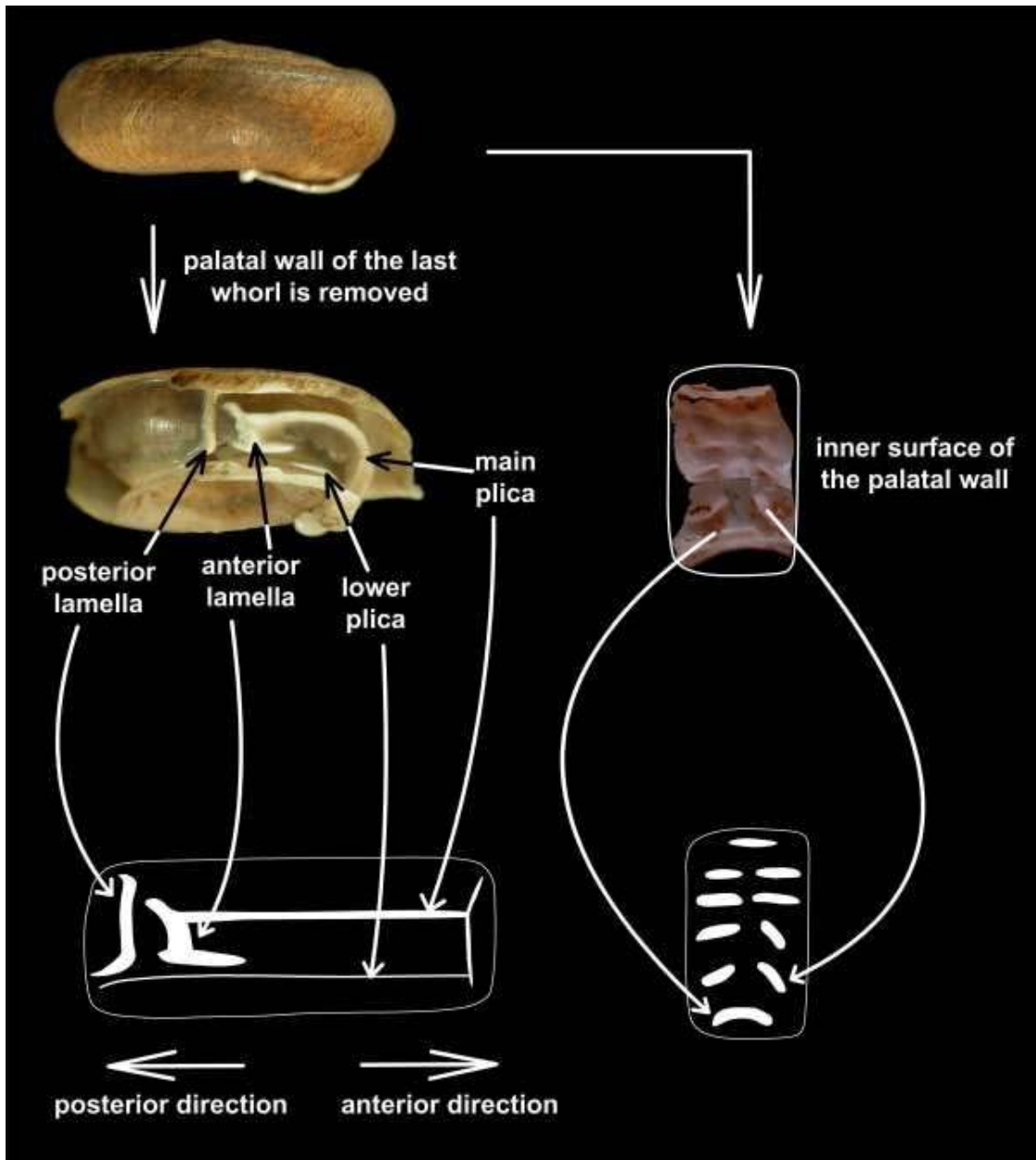


Figure 3.7. How to make the plicae and lamellae visible entirely and to present their structures-in sketches. The anterior and posterior directions are indicated.

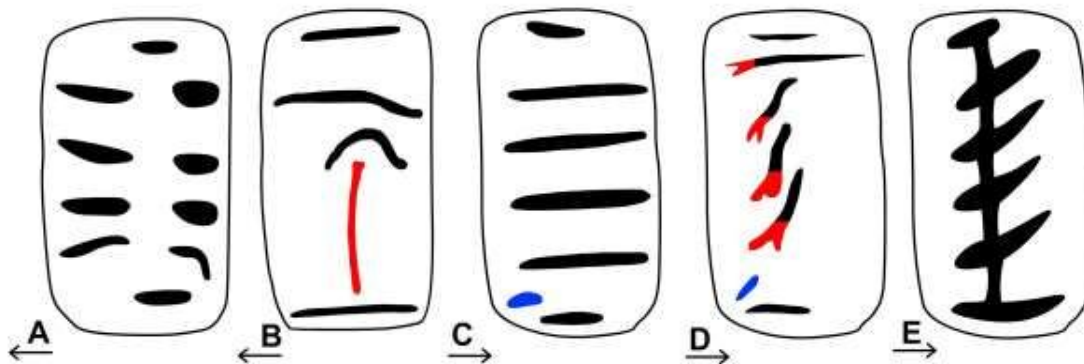


Figure 3.8. Palatal plicae of plectopylid specimens. For description of morphology, the plicae are counted from above. The additional small denticles which are usually above the posterior end of the last plicae (indicated by blue) are not counted as plicae. Small arrows below the letters indicate the direction of the aperture (anterior direction), which indicate that A and B are sinistral and the rest dextral. A: typical *Endothyrella* (plicae are divided in the middle), B: typical *Plectopylis* and *Chersaecia* (red structure indicates the vertical plate which is formed by the joint of the 4th and 5th plicae); C: typical *Sinicola* (all plicae straight, horizontal), D: typical *Gudeodiscus* (red colour indicates the dichotomously divided posterior ends of the middle plicae), E: typical *Sicradiscus* (all plicae are connected with a vertical ridge).

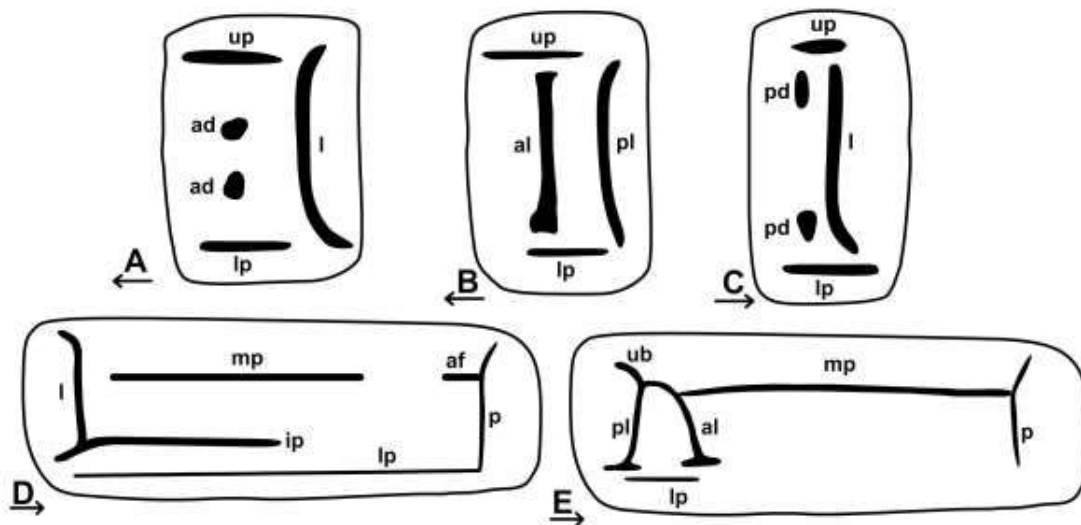


Figure 3.9. Parietal plicae (horizontal folds) and lamellae (vertical folds) of Plectopylidae. A: *Sinicola/Gudeodiscus*; B: *Gudeodiscus/Sicradiscus*; C: *Endothyrella/Sicradiscus*; D: *Chersaecia*; E: *Plectopylis*. Small arrows below the letters indicate the direction of the aperture, indicating that A, B and C are sinistral and D and E are dextral. Abbreviations: AD: anterior denticle; AF: apertural fold; AL: anterior lamella; IP: intermediate plica; L: lamella; LP: lower plica; MP: main plica; P: peristome; PD: posterior denticle; PL: posterior lamella; UB: upper branch; UP: upper plica. The "Lambda-complex" is formed by LL, RL and UB.

Terminology of the genitalia

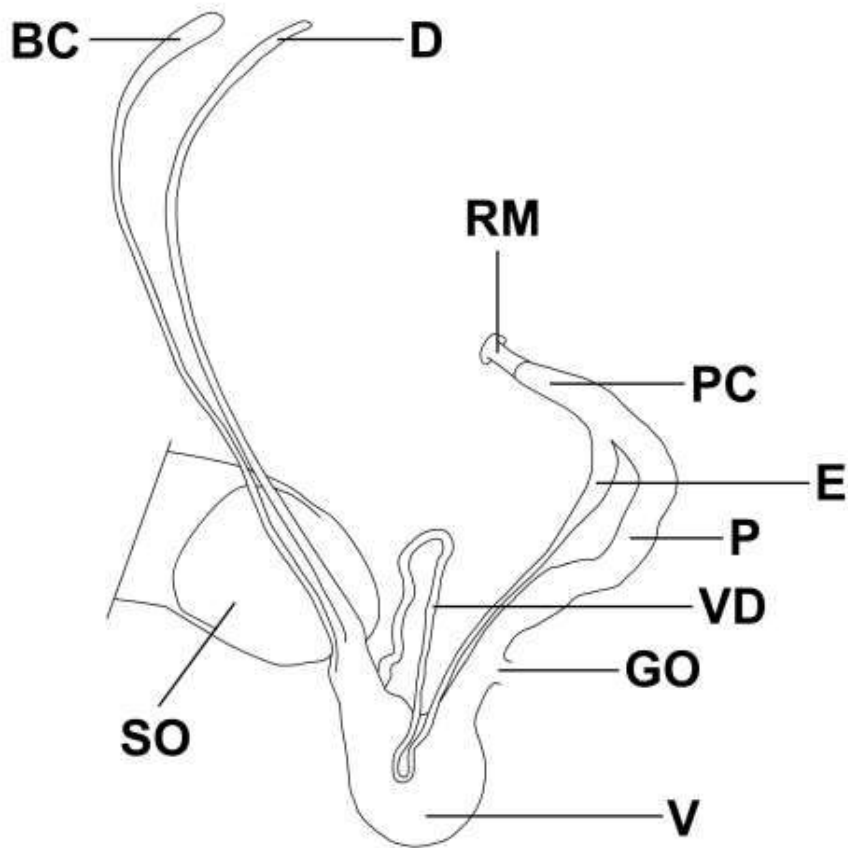


Figure 3.10. Names of reproductive organs. Abbreviations: BC: bursa copulatrix; D: diverticulum; E: epiphallus; GO: genital opening; RM: retractor muscle; P: penis; PC: penial caecum; SO: spermoviductus; V: vagina (vaginal bulb); VD: vas deferens.

Terminology of the radula

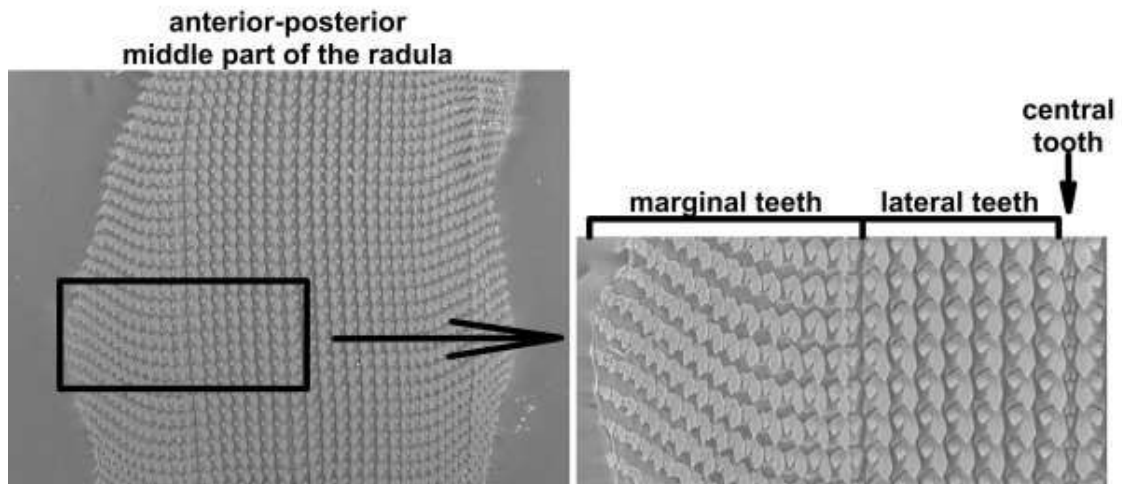


Figure 3.11. Positions of central, lateral and marginal teeth on the radula surface.

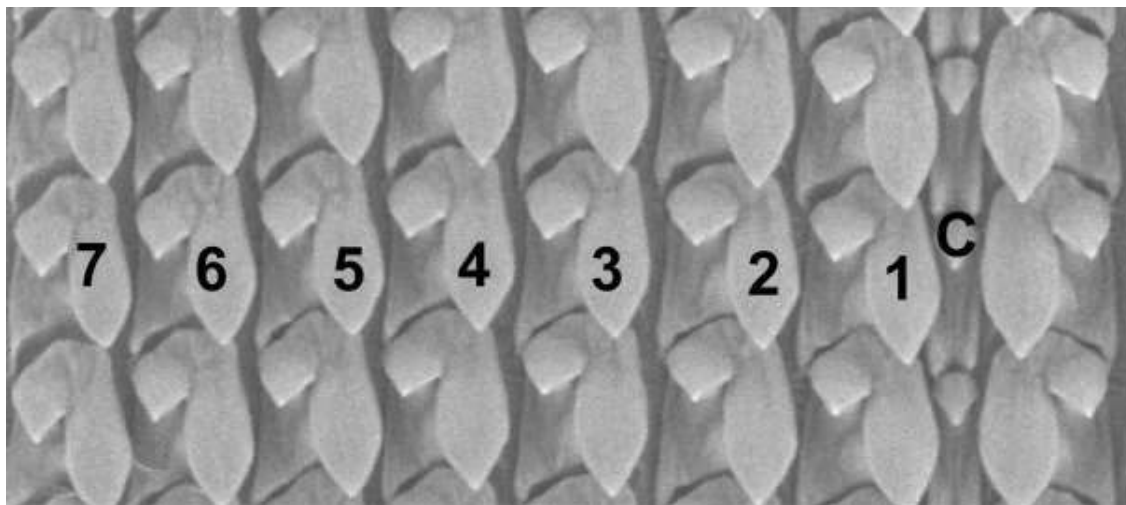


Figure 3.12. How to count the lateral teeth. Central tooth indicated by C.

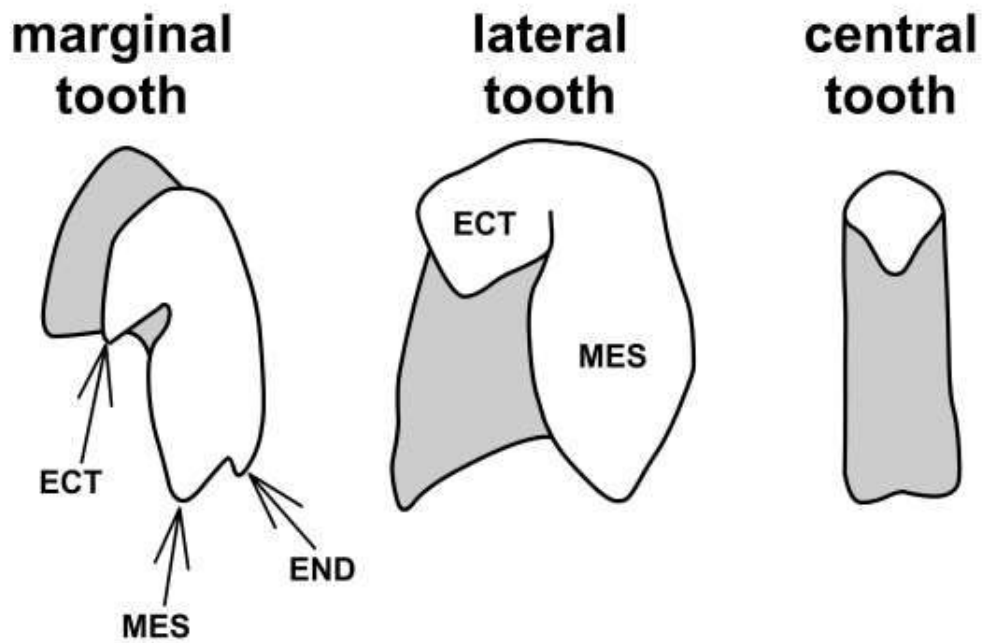


Figure 3.13. Nomenclature of tooth morphology. The figure shows a tricuspid marginal, a bicuspid lateral and a unicuspid central tooth. Abbreviations: ECT: ectocone; END: endocone; MES: mesocone. The grey shaded area indicates the base of the teeth.

Chapter 4: Assumed relatives of the family Plectopylidae

Several living and fossil land snail groups have been proposed as possible relatives of the family Plectopylidae or Corillidae. Most of these assumptions were based on conchological characters. The majority of these groups possess flat shells, and have inner plicae, lamellae or teeth. In most cases the relationships are still only speculative.

In Tillier's (1989) phenetic ascending hierarchical classification which was based on extensive morphological analysis, Corillidae (including Plectopylidae, *Craterodiscus* and *Sculptariidae*) is clustered together with Oleacinidae, Streptaxidae, and Rhytididae, and in a larger cluster it is found together with Urocoptidae, Clausiliidae, Subulinidae, Ferussaciidae and Sagdidae. In the molecular tree published by Wade et al. (2000) *Corilla* clusters with Megalobulimidae, Dorcasiidae, Caryodidae, Chlamydephoridae, Rhytididae, Acavidae, and Testacellidae. No sequence data of Plectopylidae has been published so far.

In the following I list the taxa which were mentioned as close relatives or members of Plectopylidae. In case of *Amphicoelina* and *Zilchistrophia* I reject their close relationship with the Plectopylidae based on conchological and anatomical evidence, respectively. In other taxa I rely on literature information and comment on the base of their similarities with the Plectopylidae.

Family Clausiliidae Gray 1855

Type genus: *Clausilia* Draparnaud 1805.

Remarks: Clausiliidae is probably the most speciose pulmonate family with over 1200 species (Nordsieck 2007). It is the only high-spired group which has been mentioned as a relative of the Plectopylidae. Stoliczka (1871) realized that the anatomy and the inner lamellae of *Plectopylis* (he examined *Plectopylis* and *Endothyrella* specimens) is similar to those of *Clausilia*: "I consider these internal folds to be in some respect analogous to the clausilium in *Clausilia*". He added later: "On the whole the form of the body very closely resembles that of a *Clausilia*, and a comparison on the internal organisation of the two genera also indicates their close relation".

The genital anatomy of both families (i.e. Clausiliidae and Plectopylidae) is indeed similar, but this may be due to the simple formation of both the male and female genitalia. The male part is a simple penis-epiphallus-vas deferens tube in both families, occasionally with a penial caecum. Clausiliids sometimes possess a vestigial flagellum which is always missing in Plectopylidae. The female part also lacks additional organs, such as dart sac, mucous glands and appendices. The characteristically positioned diverticulum of Plectopylidae is similar to that of the subfamily Garnieriinae. In Garnieriinae it also inserts on the the vagina-pedunculus complex, and not on the stalk of the bursa copulatrix as in all other clausiliid subfamilies and most stylommatophoran groups (Szekeres 1998).

The palatal plicae of Plectopylidae and Clausiliidae (Figure 4.1C) are situated in similar relative position, namely a quarter to a half whorl behind the aperture. These plicae can be homologous due to their similar relative positions. Most parietal plicae and lamellae of Plectopylidae have their "pair" in the Clausiliidae (Figure 4.1A–B). I also assume homology between these respective pairs, due to their identical relative positions. The plectopylid apertural fold is probably homologous with the clausiliid superior lamella (=parietalis), and the main plica is homologous with the spiral lamella (=spiralis). In some species of the Clausiliidae the parietalis and the spiralis are independent from each other. In the majority of the species however, they are fused during the development of the clausiliar apparatus. Even in those species which have joint spiralis and parietalis, they develop independently from each other and they fuse during development (Gittenberger 2000, Sulikowska-Drozd 2009, Páll-Gergely 2010). The plectopylid lower plica which runs very close to the lower suture is probably homologous with the subcolumellar lamella (subcolumellaris), and the upper parietal plica in Plectopylidae may be homologous with the parallel lamella (=parallelis) of the Clausiliidae. The clausiliid inferior lamella (=columellaris) and the clausilium may be homologous with the vertical lamellae of Plectopylidae, because they have similar positions within the shells, although the morphology of these structures are very different.

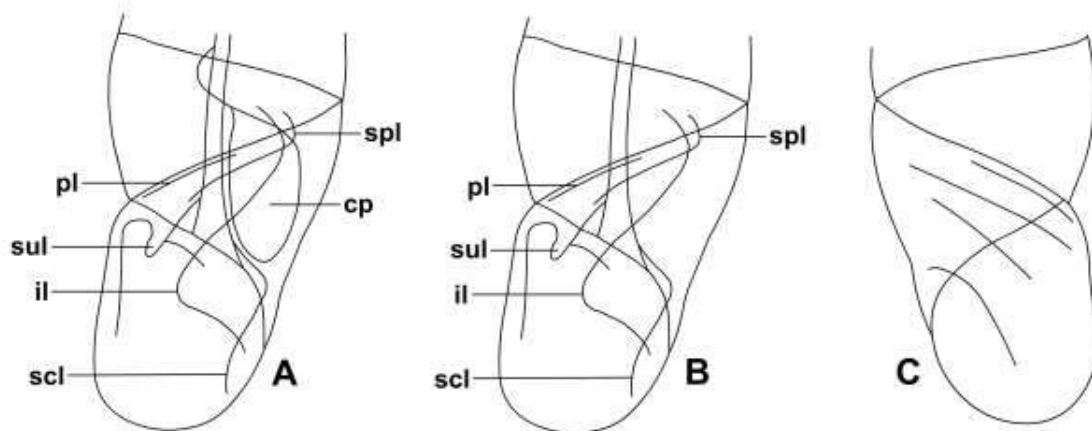


Figure 4.1. Different views of the plicae and lamellae of a clausiliid shell (after Nordsieck 1982). Figure A shows the clausiliar apparatus (CA) with the clausilium, Figure B shows the CA without clausilium, Figure C shows the palatal plicae. Abbreviations: CP: plate of the clausilium; IL: inferior lamella (columellaris), PL: parallel lamella (parallelis); SCL: subcolumellar lamella (subcolumellaris); SPL: spiral lamella (spiralis); SUL: superior lamella (parietalis).

Family Sculptariidae Degner 1923

Figure 4.2

Type genus: *Sculptaria* L. Pfeiffer 1855.

Content: Sculptariidae is a monotypic family including the single genus *Sculptaria* L. Pfeiffer 1855 (type species: *Helicodonta sculpturata* Gray 1839, with monotypy).

Diagnosis (according to Schileyko 1999): Shell lenticular, discoidal, last whorl descending in front, becoming free at aperture; often carinated; protoconch smooth; teleoconch nearly smooth or has complicated reticulated/tubercular structure due to spiral and radial lines or grooves; aperture strongly oblique, with a parietal entering lamella and 2-3 palatal plicae; umbilicus broad.

Penis thin-walled, subcylindrical, not short, with very short flagellum and small penial caecum at upper end; internally with quite conspicuous relief: one side occupied by thin, long papillae, on opposite side turning to vas deferens there are numerous deep fosses corresponding to papillae; in intact penis these structure forms a sort of valvae that may isolate upper chamber of penis from cavity of atrium; penial retractor inserts on flagellum apically; vas deferens free, entering very short, semitransparent epiphallus apically through simple pore; vagina long, cylindrical, free oviduct extremely short, spermathecal stalk slender, subcylindrical, elongated reservoir bound to spermooviduct at short distance from albumen gland; talon hidden.

Differential diagnosis: Sculptariidae is similar to Plectopylidae by the flat, widely umbilicated shells and the reticulated sculpture. The most conspicuous conchological difference is that in the Plectopylidae the armature consists of palatal and parietal plicae and lamellae approximately a quarter to a half whorl behind the aperture, only the main plica reaches the aperture in some taxa, whereas the sculptariid plicae are situated within the aperture.

The sculptariid genital system is insufficiently known. The reproductive anatomy was described in three species only: *Sculptaria collaris* (by Tillier 1989), *S. sculpturata* (by Schileyko 1999) and *S. damarensis* (by Degner 1923). Similarly to Plectopylidae, Sculptariidae also has simple genitalia. Both *S. collaris* and *S. sculpturata* lack a diverticulum and possess a penial caecum and a "flagellum" on which the retractor muscle attaches, whereas *S. damarensis* has a diverticulum which derives from the wall of the bursa copulatrix, and lacks a penial caecum and a flagellum. In contrast, most Plectopylidae has a diverticulum which derives from the wall of the distal vagina, and most species has a penial caecum on which the retractor muscle attaches. The inner structure of the penial wall is known only in *S. sculpturata* of which one side of the penis has long papillae, and the opposite has deep fosses corresponding to papillae. Plectopylid penial walls are dominated by longitudinal folds which usually form pockets for calcareous granules.

Remarks: *Sculptaria* was classified within the family Endodontidae by Pilsbry 1894 as a subgenus of *Phasis* Albers. He also noted that *Sculptaria* is a "group of problematic relationships". Degner (1923) was the first to describe the anatomy of a *Sculptaria* species. He placed the genus next to *Corilla* on the basis of anatomical similarities. Zilch (1959-1960) followed Degner, and placed *Sculptaria* within the Corillidae. Recently Schileyko (1999) classified Sculptariidae Degner 1923 in the superfamily Acavoidea Pilsbry 1894. Bouchet and Rocroi (2005) retained Sculptariidae in Plectopyloidea. The taxonomic position of the Sculptariidae is still unsolved.



Figure 4.2. *Sculptaria* sp. Namibia, Collection Cédric Audibert, Photo: Claude and Amandine Evanno.

Family Strobilopsidae Pilsbry 1918

Type genus: *Strobilops* Pilsbry 1892.

Remarks: Strobilopsidae are superficially similar to the Plectopylidae by the flat shells with internal plicae and the strongly sculptured dorsal sculpture. The genus *Enteroplax* was described by Gude (Gude 1899e) as a section of *Plectopylis*. Solem (1968) and Schileyko (1998) classified this genus to the family Strobilopsidae Wenz 1915. Strobilopsidae (both living and fossil) have one, two, or three parietal plicae (usually two) which usually reach the peristome (e.g. Pilsbry 1927, Bartha & Soós 1955, Manganelli et al. 1989, 2007, Schileyko 1998). In Corillidae only one plica (the apertural fold/main plica) reaches the peristome. Although in a few species only, Plectopylidae have two plicae reaching the peristome. The plectopylid apertural fold and main plica is probably homologous with the corresponding plicae of Strobilopsidae because of the similar respective position of them inside the shells. On the other hand, the long, lower plectopylid parietal plica is most probably not homologous with any of the plicae of Strobilopsidae, because it is situated more basally from the apertural fold than those in strobilopsids.

Molecular information showed that Strobilopsidae is the member of the clade Orthurethra, whereas *Corilla* showed up in a very different (unnamed) clade on the stylommatophoran tree (Wade et al. 2006).

Family Camaenidae Pilsbry 1893

Type genus: *Camaena* Albers 1850.

Remarks: Bradybaenidae is the junior synonym of Camaenidae (Wade et al. 2007).

Genera *Stegodera* Martens (in Pfeiffer 1876b) and *Traumatophora* Ancey 1887

Type species: *Stegodera*: *Helix angusticollis* Martens 1875 (by monotypy); *Traumatophora*: *Helix triscalpta* Martens 1875 by original designation.

Remarks: Pilsbry (1894) classified the genera *Stegodera* and *Traumatophora* as subgenera of *Plectopylis*. The single palatal sulcus of *Stegodera* and the three palatal sulci of *Traumatophora* are superficially similar to corillid or plectopylid palatal plicae, but these structures are probably not homologous. The plectopylid/corillid plicae are lime layers laid on the inner wall of the last whorl. This modification is not visible on the outer surface. Contrary, in case of *Stegodera* and *Traumatophora* the sulci are the result of longitudinal depressions of the outer surface of the last whorl. The anatomy of these monotypic genera is unknown, but they likely belong to the family Camaenidae (see Schileyko 2003).

Genus *Amphicoelina* Haas 1933

1933 *Amphicoelina* HAAS, Archiv für Molluskenkunde, 65 (4/5): 231.

2014a *Amphicoelina*, — Páll-Gergely & Asami, Genus 25(3): 553–557, Figs 22A–D.

Type species: *Helix biconcava* Heude, 1882.

Content: *biconcava* (Heude 1882), *diplomphala* (Möllendorff 1886), *omphalospira* (Möllendorff 1897) and *subobvoluta* (Ancey 1882).

Remarks: Haas (1933) erected the genus *Amphicoelina* for four Chinese *Drepanostoma*-like (*Drepanostoma* Porro 1836, family Helicodontidae) species, and chose *Helix biconcava* Heude 1882 as the type species. He proposed that the genus is closely related to *Chloritis* (now family Camaenidae, see Schileyko 2003). To my knowledge, the first author who classified *Amphicoelina* within the Corillidae was Yen (1939). Zilch (1960) followed this idea, and classified *Plectopylis*, *Corilla* and *Amphicoelina* within Corillidae. Schileyko (1999) mentioned that there is a thin parietal lamella inside the body whorl and classified the genus together with Gude's sections into the Plectopylidae. My examination, however, did not verify the presence of a vertical plate beyond the aperture (or any inner lamellae or teeth). In the collection of the SMF I examined the *Amphicoelina* shells, and found three shells with broken apertural part (i.e. the last half/quarter whorl was missing): paralectotype of *A. diplomphala*, Patung, Hupei: China, coll. Möllendorff, SMF 7018; paralectotype of *A. omphalospira*, Patung, Hupei: China, coll. Möllendorff, SMF 7016A; one corroded specimen labelled as *A. subobvoluta*, Njū-tsoū-shan, Ta-Yeh, Hupei, China, Krejci-Graf, S 1937, SMF 24755. The internal lamellae would have been visible in these shells if they were present, but I found no signs of folds. Moreover, one *Amphicoelina* specimen (China, Chensi merid., Mont Tsin-Ling (?), leg. l'Abbé David, MNHN 2012-27024) has a small hole of the last whorl which allowed us to observe the parietal wall. I again found no signs of plicae. To my knowledge, no illustrations of lamellae of *Amphicoelina* have ever been published.

The shell sculpture of *Amphicoelina* consists of extremely small (about 10–20 µm) scale-like structure as well as long, slender and cylindrical hairs (Figure 4.3C). These slender periostracal hairs are not in the spiral or radial arrangement. This sculpture clearly differs from that of Plectopylidae, which usually have the reticulated surface. Some plectopylid species (*Chersaecia dextrorsa*, several *Sinicola* and *Endothyrella* species) also possess long periostracal folds, but these are arranged in well-visible spiral lines on the body whorl. At present, our information is limited on *Amphicoelina* without anatomy of soft bodies. However, the absence of internal lamellae and the camaenid-like sculpture on shell surface suggest that *Amphicoelina* belongs to the Camaenidae as proposed by Haas (1933).

Distribution: Southern China (Hunan and Hubei).

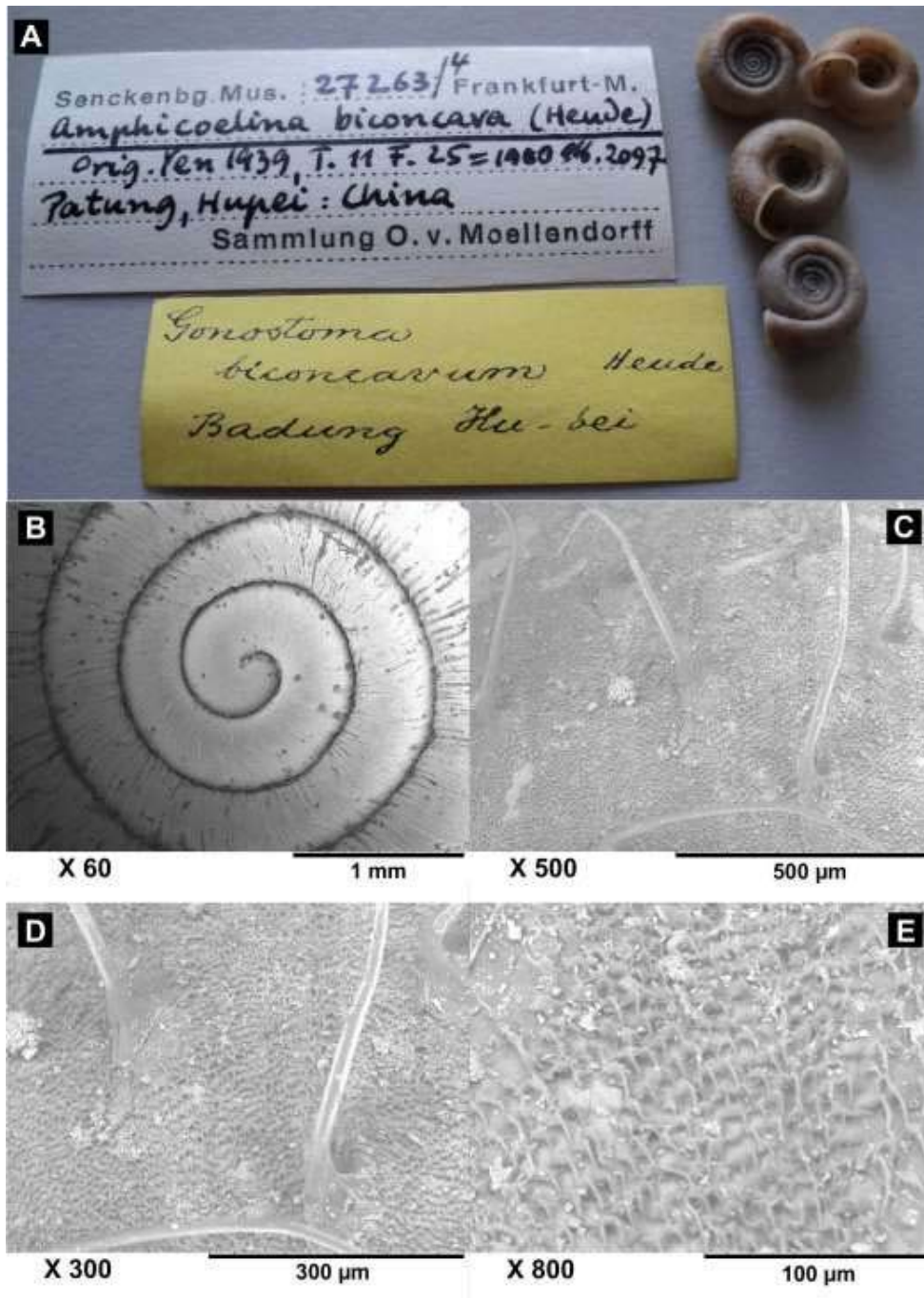


Figure 4.3 A: Sample of *Amphicoelina biconcava* (Heude 1882) in the Senckenberg Museum; B: protoconch of *Amphicoelina* sp., China, Chensi merid., Mont Tsin-Ling (?), leg. l'Abbé David, MNHN 2012-27024; C–E: sculpture of the last whorl of *Amphicoelina* sp., same data as Fig. B.

Genus *Zilchistrophia* Weyrauch 1960

1960 *Zilchistrophia* Weyrauch, Archiv für Molluskenkunde 89 (1/3): 26.

Type species: *Zilchistrophia tridentata* Weyrauch 1960, by original designation.

Remarks: See Páll-Gergely & Asami (2014b).

Genus *Craterodiscus* McMichael 1959

1959 *Craterodiscus pricei* McMichael, Journal of the Malacological Society of Australia 3: 31-32.

Remarks: McMichael (1959) described the genus *Craterodiscus*, and inferred that it may be the member of Helicarionidae because of its reduced sculpture. Tillier (1989) placed the monotypic genus in Corillidae because *Craterodiscus* lacks an oesophageal crop, which is absent in Corillidae but present in all Camaenidae, and the pulmonary complex which is similar to that of *Sculptaria* and *Plectopylis* s.l. On the other hand, *Craterodiscus* differs from all "Corillidae" by the extreme shortness of its intestine, but it may be related to the small size of *Craterodiscus*. Smith and Stanisc (1998) and Schileyko (2003) classified the genus within Camaenidae, mentioning that the simple organization of the penial complex makes the classification difficult. In the phylogenetic tree of Wade et al. (2001) *Craterodiscus* showed up in the clade of the superfamily Limacoidea, whereas Corilla was clustered in a different clade together with for instance Dorcasiidae, Megalobulimidae, Rhytididae and Acavidae.

Genus *Stenopylis* Fulton 1914

1914 *Stenopylis* Fulton, Annals and Magazine of Natural History 8 (14): 163–164.

Remarks: Haas (1945) erected the genus *Coarctatio* for *Plectopylis coarctata* Moellendorff (in Quadras & Moellendorff 1894), and placed the monotypic genus provisionally in the Streptaxidae, but mentioned that it might be a member of the Endodontidae. Solem (1957) recognized that *Planispira hemiclausa* Tate is a synonym of *Plectopylis coarctata*. Therefore, *Stenopylis* Fulton (1914) (type species: *Planispira hemiclausa*) is the valid genus for *Plectopylis coarctata*, and *Coarctatio* is a synonym of *Stenopylis*. Solem (1957) and Schileyko (2002) classified the genus in the Endodontidae. The systematic position of the genus is still unsolved, but it is certainly not a plectopylid (Solem 1957).

***Ruthvenia* Gude 1911**

Ruthvenia Gude 1911 is a replaced the name *Sykesia* Gude 1897e which replaced the name *Austenina* Gude 1897d. This genus has been introduced as a section of *Plectopylis*. Later, Gude (1914) assigned it to the Endodontidae Pilsbry, which was adopted by Schileyko (2001). Schileyko revised this classification on the basis of newly examined material, and classified *Ruthvenia* into the Charopidae Hutton.

Chapter 5: Fossil taxa assigned to the Plectopylidae

The following fossil groups with the flat shell and inner plicae have been assigned to the family Corillidae (including Plectopylidae):

- The genus *Plectopyloides* Yen 1969 from Chinese Eocene
- Proterocorilla europaea* Hrubesch 1965 from Austrian upper Cretaceous
- Three "*Anchistoma*" species from Indian Cretaceous layers (Stoliczka 1868).

I present a historical overview of the assignment of these fossils to Corillidae and Plectopylidae. In conclusion, only Chinese *Plectopyloides* Yen 1969 among these fossils should be classified to Plectopylidae. The relationship of the other two taxa of Cretaceous fossils with the Plectopylidae remains speculative.

The quotation marks for genera are widely used in palaeontology. The reason is that in many cases conchological characters are not sufficient to determine genera, which are, in living taxa, usually diagnosed based on anatomical characters.

Genus *Plectopyloides* Yen 1969

- 1969 *Plectopyloides* YEN, — Sitzungsberichte der Österreichisch Akademie der Wissenschaften (Abt.I), 177: 56.
- 1986 *Plectopyloides* (*Plectopyloides*), LI, — Professional Papers of Stratigraphy and Palaeontology, 14: 242.
- 1986 *Plectopyloides* (*Henanspirus*) LI, — Professional Papers of Stratigraphy and Palaeontology, 14: 246.
- 1986 *Plectopyloides* (*Menyinspirus*) LI, — Professional Papers of Stratigraphy and Palaeontology, 14: 244.
- 1986 *Plectopyloides* (*Yenellus*) LI, — Professional Papers of Stratigraphy and Palaeontology, 14: 245.
- 2014 *Plectopyloides* (*Yenellus*, *Henanspirus* and *Menyinspirus* are synonyms), — Páll-Gergely & Asami, Genus 25(3): 552–553, Figs 5I–P.

Remarks: Li (1986) revised the system of *Plectopyloides* Yen 1969 (type species: *Plectopyloides cretaceous* Yen 1969) after Li (1984, 1985) and Yen (1969) described plectopyloids. According to Yen (1969) the age of these fossils is Late Cretaceous, but Li (1986) argued based on other fossils (gastropods, ostracods and mammals) that they belong to the Eocene. Based on differences in the umbilicus, the palatal and parietal plicae and lamellae, Li (1986) erected three subgenera within the genus *Plectopyloides*, namely *Yenellus* (with the species *guanzhuangensis*), *Menyinspirus* (with the species *multispiralus*) and *Henanspirus* (with the species *altus*, *applanatus* and *regularus*; type species: *Plectopyloides regularus*). Li (1986) did not mention *Plectopyloides shantungensis* Yen 1969. The palatal plicae and the width of the umbilicus only slightly differ among species of this genus. In contrast, the parietal plicae and lamellae differ from one another considerably. According to Li (1986), *Plectopyloides* has one vertical lamella and three parallel horizontal plicae anterior to the lamella, and *Yenellus* a single parietal lamella, whereas *Henanspirus* and *Menyinspirus* have two vertical lamellae. In addition, *Henanspirus* has a horizontal straight plica above the first lamella, but *Menyinspirus* lacks this plica. Our revision of living Chinese Plectopylidae (Páll-Gergely & Hunyadi 2013) revealed huge diversity in palatal and parietal plication within the same genera, between subspecies or sometimes even within specimens from the same localities. All of these types in variable parietal lamellation occur within the genus *Gudeodiscus*. The parietal plicae and lamellae of *G. ursula* Páll-Gergely & Hunyadi 2013 are similar to those of the genus *Plectopyloides* (*Plectopyloides*). The "*Yenellus*-type" plication (presence of a single lamella) occurs in several species of the genus *Gudeodiscus*. Moreover, the "*Plectopyloides*-type" specimens as well as the "*Henanspirus*-type" specimens are found together with *Gudeodiscus emigrans otanii* in the same localities (Páll-Gergely & Hunyadi 2013, Páll-Gergely & Asami 2014). Accordingly, these differences, although are seemingly large, do not support taxonomical separation into multiple subgenera or in other higher ranks than species. The subgenera described by Li (1986) (*Menyinspirus*, *Yenellus* and *Henanspirus*) are synonyms of *Plectopyloides*. The taxonomic position of "*Plectopylis*" *antiquus* Yu & Pan 1982 is questionable because the inner lamellae of fossils could not be observed, and thus should be placed in the genus *Plectopyloides*.

In the original description, Li (1986) used two different spellings for each of two species; *multispiralus* and *multispiralul* for one species and *guanzhuangensis* and *guanzhangensis* for the other species. In our paper (Páll-Gergely & Asami 2014) we propose to use the names spelled as *multispiralus* and *guanzhuangensis* as the first reviser choice.

Plectopyloides and *Gudeodiscus* are more similar to each other than others, in the rounded body whorl and morphology of plicae and lamellae. *Plectopyloides* differs from *Gudeodiscus* in the conspicuously narrow umbilicus and arrangement of palatal plicae. According to the drawings of Li (1986), the lower, straight and long palatal plica

is situated anteriorly of the penultimate and curved plica. This is never the case in *Gudeodiscus*, which has the short, usually curved plica usually under the penultimate plica. In some cases, such as in *Gudeodiscus marmoreus*, the lower plica is positioned anteriorly to the other plicae, but much lower in position, unlike in *Plectopyloides*.

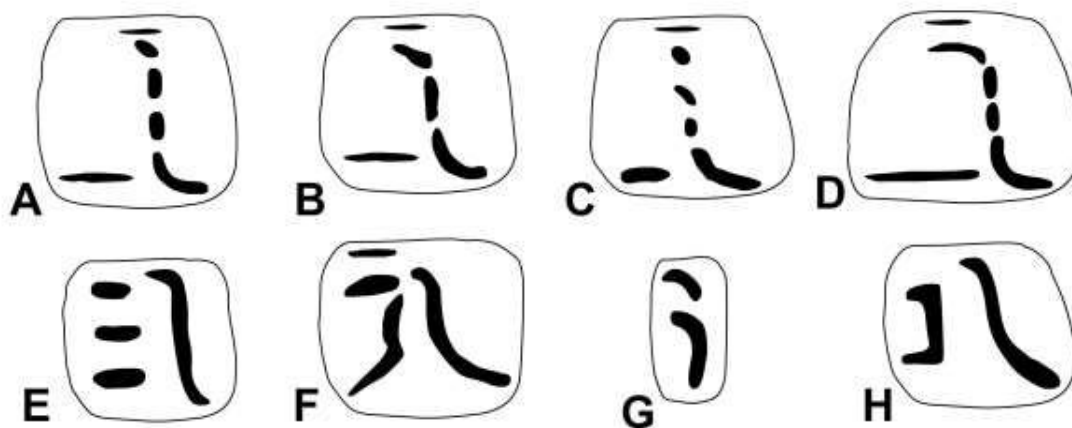


Figure 5.1. Palatal (A–D) and parietal (E–H) plication of the genus *Plectopyloides* Yen 1969 (after Li 1986). A and E: *Plectopyloides cretaceus* Yen 1969; B and F: *Plectopyloides regularus* Li 1984; C and G: *Plectopyloides guanzhuangensis* Li 1986; D and H: *Plectopyloides multispiralus* Li 1986.

Proterocorilla Hrubesch 1965 and similarly looking taxa

Remarks: *Proterocorilla europaea* was described from the Upper Cretaceous near Salzburg (Austria) and assigned to the family Corillidae (Hrubesch 1965) (including *Corilla*, *Plectopylis* and *Sculptaria*). *Proterocorilla* is characterized by a small (4 mm), flat shell with eight palatal plicae, one angular plica and three parietal plicae. The parietal plicae reach the aperture but the palatal plicae seemingly do not, although most available shells are fragments, and fully grown complete shells are rare. In contrast to the three parietal plicae of *Proterocorilla*, Corillidae have a single parietal plica (=main plica) which reaches the peristome, whereas some species of Plectopylidae have two plicae which run until the apertural rim. The homology of the plectopylid and corillid plicae and those of *Proterocorilla* is questionable. The plectopylid and corillid main plica runs approximately on the middle line of the parietal wall, whereas the plectopylid lower plica is situated very close to the lower suture. In contrast, *Proterocorilla* has the three parietal plicae situated next to each other in equal distance between each other and from both sutures.

Hrubesch (1965) mentioned that "*Helix*" *reithmuelleri* (Tausch, 1886) (Ajka, Hungary) and "*Helix*" *aigenensis* (Tausch, 1886) (Aigen, Austria) are the closest relatives. Both species were also described from late Cretaceous layers. The main difference is that *Proterocorilla* has wide umbilicus and those two "*Helix*" species have closed umbilicus. The parietal plicae of the two "*Helix*" species are, however, similar to those of *Proterocorilla*.

Oppenheim (1892) described the subgenus *Helix* (*Pseudostrobilus*) for *reithmuelleri*, and placed it next to *Strobilus* Sandberger 1872. The valid name of this is *Strobilops* Pilsbry 1892, Strobilopsidae; non *Strobilus* Anton, Achatinellidae (see Schileyko 1998). Hrubesch (1965) cited Oppenheim (1892) but did not apply the name *Pseudostrobilus* and has not classified *Proterocorilla* in Strobilopsidae. Nordsieck (1986) included both *Proterocorilla* and *Pseudostrobilus* in the family Anostomopsidae Nordsieck 1986, together with the genera *Anostomopsis* Sandberger, *Enneopsis* Wenz, *Gosavidiscus* Hrubesch 1965, *Strophostromella* Fischer, and *Eoplicadomus* Hrubesch 1965. The classification of genus *Eoplicadomus* in the Anostomopsidae is uncertain (Nordsieck 1986). Specimens of all of these genera were obtained from European Upper Cretaceous layers. They are characterized by the fold system, with several parietal and palatal folds reaching the aperture.

It is unlikely that *Proterocorilla* or any members of the European Anostomopsidae are related to the exclusively Asian families Corillidae and Plectopylidae. Their similarities (flat shells and inner plicae) are limited as outlined above, the plicae of Plectopyloidea and Anostomopsidae may not be homologous. It is more reasonable to assume that that Anostomopsidae are the ancestor of or related to Strobilopsidae, which are present in Europe with

many species at least from the Middle Eocene until the late Pliocene (Manganelli et al. 1989). The geographic origin of Strobilopsidae is a challenging problem and one of the most interesting cases in land snail biogeography (Solem 1979, 1981, Manganelli et al. 1989). They most possibly originate in the area of Laurasia corresponding with the present-day Europe (Manganelli et al. 1989). This may support the hypothesis that Strobilopsidae have evolved from Cretaceous Anostomopsidae, and that Plectopyloidea are not related to these groups. See also under Strobilopsidae in the chapter "Relatives of Plectopylidae".

"*Anchistoma*" species from India

Stoliczka (1868) described *Anchistoma cretaceum*, *A. arrialoorensis* and *A. arcotense* from Southern India (Arrialoor and Trichinopoly formations). The Arrialoor (Ariyalur) formation is of Campanian to Maastrichtian age (66–83.6 Ma) according to Sastry et al. (1968), whereas the Trichinopoly formation is of Santonian-Coniacian age (83.6–89.8 Ma, Govindan et al. 1998).

These taxa mentioned as similar to *Corilla* and *Plectopylis* by Stoliczka (1868). Nevill (1881) mentioned without formal explanation that Stoliczka's species and plectopylids belong to entirely different groups. To my knowledge, no additional publications dealt with these Indian fossils.

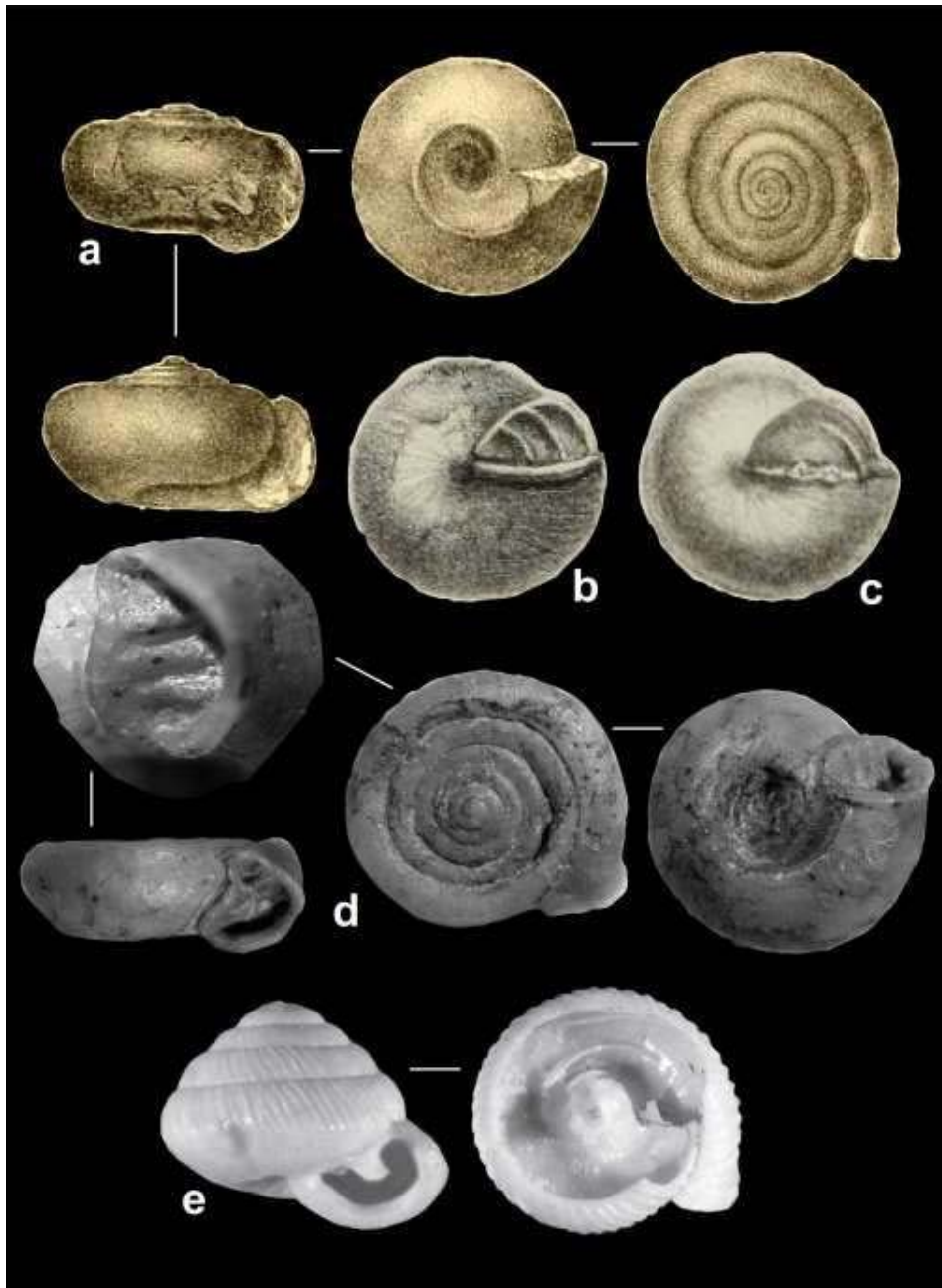


Figure 5.2. Fossil taxa assigned to Corillidae and Plectopylidae. A: "*Anchistoma*" *cretaceum* (Stoliczka 1868), "Neighbourhood of Comarapolliam, at Ninnyoor and Veraghoor", "Formation: Arrialoor group" (drawings from the original description); B: *Pseudostrobilus reithmuelleri* (Tausch 1886), "Salzburger Gosaubildung" (drawings from the original description); C: *Pseudostrobilus aigenensis* (Tausch 1886), "oberen des Csingerthales bei Ajka im Bakony", "Hangendmergel des Bernsteinflötzes" (drawings from the original description); D: *Proterocorilla europaea* Hrubesch 1965, holotype, PMM 1953 XXX 38, Photos: A. Nützel; E: *Strobilops pachychila* Soós in Bartha & Soós, 1955, Late Miocene of Öcs (Hungary), SMF 245835 (figures from Manganelli et al. 2007).

Chapter 6: Taxonomic history of the Plectopylidae

Classifications before Gude (1899e)

Helix plectostoma was the first known species which is assigned today to the Plectopylidae. That species was described by Benson (1836), who classified it within the subgenus *Helicodonta*, and mentioned that because of its angulated periphery it shows connection towards the subgenus *Helicigona*. In modern classifications *Helicodonta* and *Helicigona* belong to the family Helicodontidae and Helicidae, respectively, and both are the members of the superfamily Helicoidea (see Schileyko 2006a, 2006b). Benson (1836) compared *Helix plectostoma* with *H. personata*, (= *Isognomostoma isognomostomos* (Schröter, 1784), family Helicidae) and *H. Corcyrensis* (= *Lindholmiola corcyrensis* (Rossmässler, 1838), family Helicodontidae).

Plectopylis achatina (Pfeiffer 1845), *P. refuga* (Gould 1846) and *P. anguina* (Gould 1847) were all introduced as *Helix* species. Pfeiffer (1845) mentioned that a single shell of *Helix achatina* was part of Gray's private collection, and he referred to *H. achatina* as a species already described by Gray. He gave South America as the type locality, although his style of writing ("soll aus Südamerika herstammen") indicates that this locality was uncertain (Pfeiffer 1845). In a later book (Pfeiffer 1868) he gave the locality "Farm Caves prope Moumein", and kept publishing Burmese localities in later volumes (Pfeiffer 1878, Pfeiffer & Clessin 1881).

Gould (1846) highlighted the high similarity between *H. refuga* and *H. carabina* (= *Corilla carabina*). Albers (1850) erected the subgenus *Atopa* for *Helix achatina*, *H. refuga* and *H. rovolii* (sic!) (= *Corilla rivolii*). In the same work, *Helix plectostoma* was classified within the subgenus *Gonostoma*. *Atopa* Albers 1850 was a junior homonym of *Atopa* Fabricius 1799 (Coleoptera), therefore Adams and Adams (1855) proposed *Corilla* (a subgenus of *Anchistoma*) for replacement. In face of this, the name *Atopa* was in use for over 20 years (Tryon 1887). Addition to the three species mentioned by Albers (1850), Adams & Adams (1855) included *Helix erroneum* to the subgenus *Corilla*.

Additional four plectopylid species have been described in the 1850's: *Helix repercussa* (Gould 1856) *H. cyclaspis* (Benson 1859c, new name for *Helix catinus* Benson 1859a), *H. pinacis* (Benson 1859) and *Corilla pulvinaris* (Gould 1859). The latter species was described from Hong Kong, the first species outside of India and Burma.

The helicid subgenus *Plectopylis* was erected by Benson (1860a), who realized that *Plectopylis* species possesses a "strong vertical lamina", whereas *Corilla* has only "few lamellae running longitudinally to a moderate distance within the aperture". Benson (1860a) classified six species within *Plectopylis* (*achatina*, *cyclaspis*, *refuga*, *leiophis*, *plectostoma*, *pinacis*), and subdivided the group into three "sections", without naming them. The first section is equivalent with the genus *Plectopylis* in modern sense, and contained *H. achatina* and *H. cyclaspis*. The second section (*Chersaecia* in Gude's 1899e system) contained *Helix refuga* *H. refuga* var. *dextrorsa* and *H. leiophis*. The third section, which is equivalent with Gude's (1899e) *Endothyra*, contained *H. plectostoma* and *H. pinacis*.

Pfeiffer (1878) and Pfeiffer and Clessin (1881) classified all known Plectopylidae species within the section *Plectopylis* (genus *Helix*), but included *Helix pettos* and *H. pulvinaris* in the subsection *Corilla*, section *Ophiogyra* Albers 1850. Between 1881 and 1887 several species were described from China (Möllendorff 1882, 1883, 1885a, 1885b, 1886, Heude 1882, 1885, Gredler 1881, 1887, Martens 1875, Ancy 1885). Tryon (1887) classified *Helix pettos*, *H. pulvinaris* and all Chinese species together with all *Corilla* species into the subsection *Atopa* (section *Atopa*), and classified the rest of plectopylids in the subsection *Plectopylis* (also section *Atopa*). Pilsbry (1894–1895) used *Plectopylis* on genus level, and subdivided into three subgenera: *Plectopylis*, *Traumatophora* and *Stegodera*. I discuss the latter two subgenera separately under the "Relatives of Plectopylidae". Pilsbry (1894–1895) classified all species which are now assigned to *Corilla* separately from *Plectopylis*, also on species level. In his system all species I classify within the Plectopylidae have been included in the genus *Plectopylis*.

Gude's (1899e) system

Gude (1899e) revised the whole genus *Plectopylis*, and excluded the two genera (*Traumatophora* and *Stegodera*) that Pilsbry (1894) placed in the genus. Gude (1899e) subdivided the genus *Plectopylis* into seven sections (subgenera): *Endothyra* (replaced by *Endothyrella* by Zilch 1960), *Chersaecia*, *Endoplön*, *Plectopylis*, *Sinicola*, *Enteroplax* and *Sykesia* Gude 1897e. Present knowledge clarifies that the latter two do not belong to the family Plectopylidae. I list them separately in the chapter "Relatives of Plectopylidae".

Gude's subdivision (1899e) is based on the direction of the coiling of the shell, the depth of the umbilicus, and the morphology of the palatal folds.

The diagnoses of Gude's (1899e) genera were the following:

Endothyra: "Sinistral. Umbilicus moderate. Palatal folds horizontal or oblique"

Chersaecia: "Sinistral or dextral. Umbilicus wide. Palatal folds horizontal or oblique. Sometimes with one oblique or vertical plate"

Endoplou: "Dextral. Palatal folds horizontal, oblique or almost vertical"

Plectopylis: "Sinistral. Shell flattened. Palatal armature: one vertical plate with three horizontal folds above, one below"

Sinicola: "Dextral. Palatal folds horizontal"

Classification after Gude (1899e)

After his revision, Gude continued publishing new taxa and observations of the genus *Plectopylis*. He often has not specified the subgenera of the new species he introduced (Gude 1901b, 1909). In one publication (Gude 1908b) some new species were introduced without subgeneric division, and in others the subgenera were mentioned only "hidden" in the text, instead of in the heading of the new species. In the same publication he also expressed that two newly described species which belong to the section *Sinicola*, "connect the section to *Endoplou*". From the text it is not possible to decide which two species he thought about.

In the last publication of Gude in which he described new species (Gude 1915) his decision of the subgenera were exclusively based on the morphology of the palatal plicae, which resulted in the placement of Northeastern Indian species into subgenera which were known to inhabit China, Southern Myanmar and Vietnam only.

Following Gude's activity, only few papers reported new plectopylid taxa (Ehrmann 1922, Yen 1937, 1939, Kuroda 1941, Solem 1966). These publications, however, have not criticized the system of Gude (1899e). Yen (1939) classified the genus *Amphicoelina* Haas 1933 in the Plectopylidae, which was followed by all authors (see separately under the "relatives of Plectopylidae").

Schileyko (1999) elevated all of Gude's subgenera on genus level without comments. In his system, the family Plectopylidae is composed of Gude's five genera (*Endothyrella*, *Chersaecia*, *Endoplou*, *Plectopylis*, *Sinicola*) and *Amphicoelina*.

Chapter 7: Systematics of Plectopyloidea

Superfamily Plectopyloidea

1898 Plectopylidae (pro family) Möllendorff, O. F. von, Abhandlungen der Naturforschenden Gesellschaft zu Görlitz, 22: 147.

Diagnosis (according to Schileyko 1999 and Tillier 1989): Shell dextral or sinistral, small (5–40 mm), depressed to flat, embryonic whorls only slightly enlarged. Last whorl (up to half whorl behind the aperture) with conspicuous complex system of lamellae and plicae on both the palatal and parietal sides; jaw aulacognathous, thin, slightly striated, with or without weak median projection; kidney mesurethral primary ureter completed, secondary ureter open, as ciliary groove; genital system simple, penis with or without verge, internally with in some genera with disposable calcareous granules which may play a role during mating; epiphallus present or absent (usually present), retractor muscle rare absent, flagellum rarely present, penial caecum present or absent; vagina of various length, gametolytic sac long with slightly thickened gametolytic sac, diverticulum present or absent, in Plectopylidae derived from the wall of the free oviduct.

Content: Corillidae and Plectopylidae.

Family Corillidae Pilsbry 1905

Figure 7.1

1905 Corillidae Pilsbry, Proceedings of the Malacological Society of London, 6: 289.

Type genus: *Corilla* H. & A. Adams 1885, nom. nov. pro *Atopa* Albers 1850, non *Atopa* Fabricius 1799 (Coleoptera).

Content: Corillidae is a monotypic family including the genus *Corilla* Pilsbry 1905 (type species: *Helix erronea* Albers 1853, subsequent designation by Pilsbry 1893).

Diagnosis: Shell dextral, medium to large sized (15–30 mm), flat, outline oval, body whorl rounded or shouldered; shell surface with radial ribs, spiral lines missing; ventral side usually less strongly sculptured than the dorsal; multiple armatures built during growth, the last one is just behind the aperture; parietal wall with two-three horizontal, but not straight plicae which are sometimes connected to each other; palatal wall usually with four or five straight or oblique, more or less parallel plicae; aperture sometimes with basal thickening. The plicae are entirely missing in two species.

Genitalia (after Schileyko 1999): Talon hidden or exposed, minute; vas deferens narrow, long, entering long cylindrical epiphallus apically or subapically and laterally; penis relatively short, internally with relief of conic or short corrugated tubercles and well-developed, rod-like verge which has a permanent principal longitudinal groove and a number of accidental, shallower grooves; penial retractor originating on columellar muscle and inserted onto epiphallus somewhat lower from its middle; free oviduct and vagina moderately long, subequal; spermathecal stalk long, cylindrical reservoir elongated, reaching albumen gland. See also Remarks.

Differential diagnosis: See under Plectopylidae.

Distribution: One species lives in Southern India, all others inhabit Ceylon (Sri Lanka) (Gude 1914b).

Remarks: *Corilla* (= Corillidae) and *Plectopylis* (= Plectopylidae) has been mentioned as the relatives of each other in all systems (Gude 1914b, Zilch 1959–1960, Schileyko 1999, Bouchet & Rocroi 2005). Schileyko (1999) classified only these two families in a single superfamily (Plectopyloidea), whereas others (e.g. Zilch 1959–1960, Bouchet & Rocroi 2005) included Sculptariidae as well in this superfamily.

Godwin-Austen (1889–1914) described the genital anatomy of *Corilla gudei* Sykes, whereas the genital anatomy of *C. erronea* was described by Pilsbry (1894–1895) and Schileyko (1999). The most conspicuous differences between the two descriptions of *Corilla erronea* is the presence (Pilsbry) and absence (Schileyko) of a diverticulum. It is unknown whether this is due to intraspecific dimorphism or one of the specimens was misidentified.

Family Plectopylidae Möllendorff 1898

1898 Plectopylidae Möllendorff, O. F. von, Abhandlungen der Naturforschenden Gesellschaft zu Görlitz, 22: 147.

Type genus: *Plectopylis* Benson 1860.

Content: Subfamily1 and Subfamily2.

Diagnosis: Shell sinistral or dextral, small to medium sized (5–35 mm); flat or conical; dorsal surface usually with reticulated structure (spiral and radial lines); ventral side usually with less prominent sculpture; multiple armatures built during growth, the last one is 0.25–0.5 whorls behind the aperture, parietal wall with one or two vertical lamellae, usually with additional horizontal plicae above and below the lamellae or anterior to them; palatal wall with 6–7 plicae which sometimes fuse to each other or are divided to two parts.

Penis without verge, internally with more or less parallel fold; between the folds calcareous crystals may be found; epiphallus usually present, in most cases bound to the penis by weak fibres; penial caecum present or absent, retractor muscle usually present, attaches on the penial caecum or at the penis-epiphallus transition; vas deferens long, usually thickened before reaching the spermoviductus; vagina well-developed, sometimes with thickened "vaginal bulb"; vagina (usually up to the beginning of the gametolytic sac) with fibres which attaches it to the body wall and the diaphragm; spermoviductus long with slightly thickened gametolytic sac; diverticulum starts near the gametolytic sac; all species ovoviviparous, embryo sac with several small calcareous crystals on its surface; talon small.

Differential diagnosis: Plectopylidae differs from Corillidae by the presence of one or two vertical parietal lamellae, whereas corillids have only horizontal plicae on the parietal wall. Corillid shell lack spiral sculpture which is present in most plectopylid shells. Corillidae has penial verge, epiphallus much longer than in Plectopylidae, diverticulum (if present) derives from the wall of the gametolytic sac, whereas Plectopylidae lacks the penial verge, its epiphallus (if present) is shorter and the diverticulum originates at the base of the spermoviductus.

Distribution: The family Plectopylidae extends from Nepal and Northeastern India through large part of Southeastern Asia (including the Malay Peninsula, Northern Thailand, Northern Vietnam, Central and Southern China) to Taiwan and Southern Japan.

Subfamily1 Páll-Gergely, new subfamily

Type genus: Genus1 u. gen.

Diagnosis: Same as in Genus1 u. gen.

Differential diagnosis: Same as in Genus1 u. gen.

Content: Genus1 u. gen.

Genus1 u. gen.

Type species: *Helix refuga* var. *dextrorsa* Benson 1860.

Content: *austeni* (Gude 1899), *dextrorsa* (Benson 1860).

Diagnosis: Shell dextral, flat, widely umbilicated. Protoconch matt or dominated by tubercles (cell-like structure), shell with strong periostracal folds of the upper edge of the whorls which results in a dense reticulated fold structure at the sutures; parietal wall with a single lamella and one or two vertical plicae anteriorly. The main plica is free from the apertural fold or is in contact with it.

There is a small papilla-like organ near the atrium with unknown homology, having its own retractor muscle. The right ommatophoral retractor does not cross penis and vagina, but passes between the small papilla-like organ and the penis and vagina. The penis-epiphallus-vas deferens complex is a long, thick-walled tube which is of approximately the same length from its beginning to its end, without any notable inner structure. Retractor muscle of the penis is absent.

Differential diagnosis: The shell is similar to *Chersaecia* but differs in the coiling direction, which is dextral in Genus1 and sinistral in *Chersaecia*. No *Chersaecia* species are known to exhibit periostracal folds, whereas fine periostracal filaments (Genus1 *austeni*) and flat, large periostracal folds (Genus1 *dextrorsa*) are characteristic features of Genus1 species.

Genus1 has a penis-epiphallus-vas deferens tube which is of equal thickness from the beginning until the end. All other plectopylid species have a well-distinguishable penis and vas deferens and in most cases a separate epiphallus. The ommatophoral retractor passes next to the penis and vagina in Genus1, but runs between these organs in all other plectopylids. Genus1 lacks a retractor muscle of the penis, which was found in all other plectopylid species. Moreover, the blindly ending short organ with its own retractor muscle is known only in Genus1.

Distribution: Genus1 *dextrorsa* is known from Myanmar, whereas *D. (?) austeni* has been reported from Assam, Northeastern India (Figure 7.125).

Remarks: The anatomy of only Genus1 *dextrorsa* is known.

Genus1 (?) *austeni* (Gude 1899)

Figures 7.2, 7.29

1899c *Plectopylis austeni* Gude, Science Gossip, 6: 15, Fig. 97. ["Diyung Valley, Singpho, Assam"]

1899e *Plectopylis (Chersaecia) austeni*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Chersaecia) austeni*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Chersaecia) austeni*, — Gude, The Fauna of British India (...): 90–91, Fig. 38.

Types: The type lot (Diyung valley, Singpho Hills, Assam, leg. Ogle, NHMUK 1903.06.01.1014) contains an adult and one juvenile shell of *Plectopylis austeni*. It also contains a sinistral shell, similar to the holotype of *Plectopylis leucochila*, which probably got there accidentally. Because of the mixed sample, the adult shell of *Plectopylis austeni* is selected as the lectotype.

Diagnosis: A flat, dextral yellowish species with very coarse reticulated sculpture, elevated callus, strong apertural fold, a single lamella on the parietal side with a short main plica free from the apertural fold and an even shorter, intermediate plica under the main plica.

Description of the type series: Shell dextral, flat, dorsal surface concave, yellowish; the 6.25–6.75 whorls (n=2) are separated by a very deep suture (first whorl has shallow suture). Protoconch matt, almost smooth, irregularly wrinkled; teleoconch roughly reticulated, on the dorsal side and inside the umbilicus the spiral lines are dominant, whereas on the edge of the last whorl rather the radial lines; fine periostracal filaments are attached to the ribs; dorsal and ventral sides of every whorl flat, the boundary between the rounded edge of the body whorl and the flat dorsal and ventral sides are indicated with a shallow groove, aperture oval, peristome thickened and slightly reflexed; callus well-developed, elevated, highest at its middle; there are two canals at both ends of the callus at the joining points with the peristome; apertural fold low, free from the callus; approximately as long as the callus.

The type sample contained 3 shells, two adults (one of them opened), and an opened juvenile. Parietal wall with a curved lamella having a main plica in the middle line of the lamella; the main plica is slightly longer than the lamella; there is an additional lower, short plica (denticle) under the posterior end of the main plica; the juvenile shell had only the main plica anterior to the lamella; palatal plicae 6; the first and last are straight and free, the middle ones are oblique, short and connected by a ridge.

Measurements (in mm): D= 17–19.5, H= 5–6 (n=2).

Differential diagnosis: *D. (?) austeni* is most similar to Genus1 *dextrorsa*, which is darker, has longer main and middle parietal plicae, and its palatal plica are usually divided in the middle and not connected by a ridge.

Distribution: Genus1 (?) *austeni* is known from the type locality only (Figure 7.125).

Remarks: Without knowing the anatomy the systematic position of the species is questionable. It is placed in this genus due to the dextral shell, strong periostracal folds on the dorsal surface and the parietal lamellation which is similar to that of Genus1 *dextrorsa*.

Genus1 *dextrorsa* (Benson 1860)

Figures 7.2, 7.29, 7.32, 7.51, 7.97

1860 *Helix refuga* var. *dextrorsa* Benson, Annals and Magazine of Natural History, 3 (5), 246–247 [Phye-thán in the Tenasserim Valley].

1870 *Helix (Plectopylis) refuga* var. *dextrorsa*, — Hanley & Theobald, Conchologia Indica...: Plate 13, Figs 9.

1875a *Helix (Plectopylis) dextrorsa*, — Godwin-Austen, Proceedings of the Zoological Society of London: 44.

1875b *Helix (Plectopylis) refuga* var. *dextrorsa*, Godwin-Austen, Proceedings of the Zoological Society of London: 613.

1878a *Helix (Plectopylis) dextrorsa*, — Nevill, Hand list of Mollusca in the Indian Museum: 70.

1879a *Helix (Plectopylis) brachydiscus* Godwin-Austen, Journal of the Asiatic Society of Bengal, 48 (2): 1–3, plate 1. Fig. 1. [Mulé-it, east of Moulmein, Tenasserim]. **new synonym**

1887 *Helix (Plectopylis) brachydiscus*, — Tryon, Manual of Conchology (...): 162, Plate 36, Figs 32, 34.

1887 *Helix (Plectopylis) refuga* Var. *dextrorsa* ("Austen"), — Tryon, Manual of Conchology (...): 164, Plate 35, Fig. 2.

1896d *Plectopylis dextrorsa*, — Gude, Science Gossip, 3: 156, Fig. 21.

1896d *Plectopylis brachydiscus*, — Gude, Science Gossip, 3: 154–155, Fig. 18.

1899e *Plectopylis (Chersaecia) dextrorsa*, — Gude, Science Gossip, 6: 148.

- 1899e *Plectopylis (Chersaecia) brachydiscus*, — Gude, Science Gossip, 6: 148.
 1899f *Plectopylis (Chersaecia) dextrorsa*, — Gude, Science Gossip, 6: 175.
 1899f *Plectopylis (Chersaecia) brachydiscus*, — Gude, Science Gossip, 6: 175.
 1914b *Plectopylis (Chersaecia) dextrorsa*, — Gude, The Fauna of British India (...): 110–111, Fig. 52.
 1914b *Plectopylis (Chersaecia) brachydiscus*, — Gude, The Fauna of British India (...): 108–110, Fig. 51.

Types: Tianoba, Mulé-it Range, Tenasserim, leg. Limborg, NHMUK (12 syntypes of *brachydiscus*); Tenasserim valley, NHMUK 1906.2.2.144 (holotype of *dextrorsa*).

Museum material examined: Moulmein, coll. Möllendorff, SMF 150118/2; Siam: Ponekai, coll. Möllendorff, SMF 150120/4; Tavoy, Tenasserim, coll. Möllendorff, SMF 150119/7; Tenasserim, NHMUK 1888.12.4.1557–1559/3; Tenasserim, leg. Limborg, NHMUK/many corroded, whitish shells; Tenasserim, NHMUK 1893.4.7.1–2/2 juvenile shells.

Diagnosis: A dextral, more or less flat species with periostracal folds on the upper edge of the body whorl, callus well-developed, apertural fold present, main plica short (not reaching the apertural fold) or long (in contact with the apertural fold); palatal plicae free, most of them divided in the middle; parietal wall with a single lamella and an intermediate plica attached to its lower end.

Description of the type series of *brachydiscus*: The entirely flat or almost flat, dextral shell is light to dark brown. Most available shells (type series, NHMUK) are corroded and lost their original colour and periostracum. The 6–6.75 whorls (n=5) are separated by a deep suture. In face of the deep suture, the upper surface seems to be flat due to the flat whorls and the periostracal folds which lean on the suture. Protoconch irregularly wrinkled with extremely fine cellular structure which is sometimes not visible, or visible only on a small part of the protoconch. The teleoconch is ribbed and spirally striated, giving the sculpture a reticulated appearance. The ribs may be covered by deciduous folds of the periostracum (on fresh shells). On the dorsal surface of the whorls there are 8–9 spiral lines. The ribs are much denser than the spiral lines. The sculpture is also visible on the ventral side and inside the umbilicus. The periostracal filaments are longer near the sutures, whereas in case of two subadult specimens the periostracal filaments around the edge of the body whorl are very long, similar to those of the genus *Sinicola*. The apertural margin is white, conspicuously thickened and slightly reflexed. The parietal callus is slightly S-shaped and has two channels at the meeting point with the lip. The prominent apertural fold is approximately half as long as the callus, and is free from the main parietal plica.

Five specimens were opened. On the parietal wall there is a short vertical lamella, which is joined to a horizontal plica below. This plica is almost twice as long as the lamella and extends anteriorly. Above this plica there is a second longer plica (main plica), which is positioned at about half the height of the lamella and runs in the direction of the aperture, but stays always free from the apertural fold. In two old specimens of the type series the two plicae were almost joining. Two shells had a short plica under the lamella. On the palatal wall there are 6 plicae, the first three are more or less straight, sometimes with additional posterior small denticle; the second one usually has a dichotomically-divided posterior end; the fourth and fifth plicae are divided, their posterior portions descending downwards; the anterior portion of the 5th plica can be missing.

Differential diagnosis: See under Genus1 *austeni*.

Measurements (in mm): D= 16, H= 5.8 (holotype of *dextrorsa*); D= 16.8–19.7, H= 5.9–7.2 (n=4, type series of *brachydiscus*).

Characters of the genital system: Two specimens were dissected. Sample information: Mulé-it, east of Moulmein, Tenasserim, coll. Godwin-Austen, NHMUK 1901.4.2.10.

A small, blind-ended organ is present near the genital opening. The right ommatophoral retractor passes next to the penis and vagina, between the penis and vagina and the small blindly ended organ. A muscle consisting of a slender proximal and a thicker distal part of equal length connects this organ to the diaphragm. The penis and epiphallus, which are not well defined from each other, are very long, cylindrical and cable-like, and continue to an almost equally thick vas deferens. No retractor muscle was observed. The vagina is as thick as the penis and epiphallus, and also very long; its length is about half that of the penis and epiphallus together. Weak fibres are attached to the vagina. The gametolytic sac is about as long as the vagina. The diverticulum contained a spermatophore. The end of the spermatophore was found in the stalk of the gametolytic sac.

Radula: Figure 7.97 and Table 7.4.

Distribution: The species is known from Eastern Burma (Figure 7.125).

Remarks: The holotype of *dextrorsa* has a somewhat reversed trapezoid shape from apertural view, whereas typical *brachydiscus* specimens have a rounded body whorl. The value of this character is unknown due to the single available shell of *P. dextrorsa*. The apertural fold of some typical *brachydiscus* specimens starts from a small

distance from the callus, or it is slightly connected to it. In the holotype however, the apertural folds starts from the callus. The specimens assigned to *Plectopylis brachydiscus* and *P. dextrorsa* can mainly be distinguished by the fused (*dextrorsa*) or independent (*brachydiscus*) apertural fold and main plica. The old specimens (i.e. shells with very much thickened peristome) of the type series of *Plectopylis brachydiscus* have the apertural fold and the main plica almost reaching each other. To my understanding, this character is minor and without other stable shell characters does not allow the separation of two species.

Only the holotype of *Helix (Plectopylis) refuga* var. *dextrorsa* was found in the NHMUK, which is an intact shell without holes to observe the parietal wall. More material was probably examined by previous authors because the inner plicae and lamellae have been described.

Subfamily2, new subfamily

Type tribe: Tribe1 new tribus.

Content: Tribe1 and Tribe2.

Diagnosis: Radula and shell characters do not differ from Subfamily1. Ommatophoral retractor crosses penis and vagina; penis, epiphallus (if present) and vas deferens are distinct organs; retractor muscle of the penis present.

Differential diagnosis: See under Genus1.

Tribel, new tribus

Type genus: *Plectopylis* Benson 1860.

Content: *Endoplon*, *Chersaecia*, *Plectopylis*.

Diagnosis: Shell primarily sinistral (some species are dextral), flat, widely umbilicated; protoconch matt or dominated by tubercles (cell-like structure), usually with irregularly, roughly growth lines, wrinkled; parietal wall with one or two vertical lamellae and usually long horizontal plicae anteriorly to the lamellae.

Ommatophoral retractor passes between penis and vagina; epiphallus may be absent, penis, epiphallus (if present) and vas deferens are easily distinguishable; retractor muscle attaches on the distal end of the penis; penial caecum absent, or very minute; inner penial wall with wavy parallel folds, sometimes with calcareous granules in the penial lumen; epiphallus internally with straight, parallel folds; diverticulum usually much shorter than the gametolytic sac.

Differential diagnosis: The other tribe of Subfamily2, Tribe2 usually lacks long lower and main plicae, and they usually have ribbed protoconchs; most species of Tribe2 possess a well-developed penial caecum and the diverticulum (when present) is as long as the gametolytic sac.

Content: *Chersaecia* Gude 1899a, *Endoplon* Gude 1899a (?) and *Plectopylis* Benson 1860.

Genus *Chersaecia* Gude 1899

1899e *Chersaecia* Gude, Science Gossip, 6: 148.

Type species: *Plectopylis Leiophis* Benson1860a by original designation. *Plectopylis leiophis* is the synonym of *Helix refuga*, therefore *H. refuga* Gould 1846 is the type species of *Chersaecia*.

Content: *goniobathmos* Ehrmann 1922, *kengtungensis* (Gude 1914), *species1* u. sp., *perarcta* (Blanford 1865), *perrierae* (Gude 1898a), *refuga* (Gould 1846), *shanensis* (Stoliczka 1873), *shiroiensis* (Godwin-Austen 1875), *woodthorpei* Gude 1899.

Diagnosis: Shell sinistral, flat, widely umbilicated; in most cases protoconch seemingly "smooth", but never shiny, matt or with tubercles of various size; aperture always with fold; parietal wall with one or two vertical lamellae and usually one or two long horizontal plicae reaching the callus (main and lower plica); palatal plicae all horizontal, sometimes divided in the middle, in some species with several additional denticles posteriorly, in some species similar to that of *Plectopylis* (three horizontal plicae above and one below the vertical plate formed by the accretion of two plicae).

Genitalia typical of that of the tribe Tribe1. Epiphallus present or absent.

Differential diagnosis: *Chersaecia* differs from *Endothyrella*, *Sinicola*, *Gudeodiscus* and *Sicradiscus* by the usually tuberculated (not regularly ribbed) protoconch and the presence of long palatal plica running until the parietal callus. For the delimitation of *Chersaecia* from the genera *Plectopylis* and *Endoplon* see Remarks under *Chersaecia* and *Endoplon*. See also under *Endothyrella*.

Distribution: The genus *Chersaecia* is known from Northeastern India, Myanmar and Northern Thailand (Figure 7.129).

Remarks: The diagnosis of *Chersaecia* in the original description (Gude 1899e) was the following: "Sinistral or dextral. Umbilicus wide. Palatal folds horizontal or oblique. Sometimes with one or oblique or vertical plate.", whereas the diagnosis of *Plectopylis* s.s. was given as follows: "Sinistral. Shell flattened. Palatal armature: one vertical plate with three horizontal folds above, one below". However, the fusion of the 4th and 5th palatal plicae into a vertical plate, which is very characteristic in *Plectopylis*, also present in two species (*perrieriae*, *shiroiensis*) which were assigned to *Chersaecia* by Gude (1899e). Therefore this character state cannot be used as a distinguishing character between the two genera. The peculiarity of Gude's division is that all *Plectopylis* species have two lamellae (they sometimes connect at their upper end), whereas all *Chersaecia* have only one lamella. These character states, however, were not mentioned by Gude (1899e), but were by Benson (1860a). Gude (1914b) referred to *Plectopylis woodthorpei* Gude 1899 as the transitional form between *Plectopylis* and *Chersaecia*, probably because of the small size of the species, which is similar to *Chersaecia*, but the presence of two lamellae, which is characteristic of *Plectopylis* sensu Gude (1899e). Some specimens of *Chersaecia perrieriae* show intermediate character state between the one and two lamellae types. Moreover, the main difference between typical *Chersaecia leiophis* and *Plectopylis goniobathmos* is absence (*leiophis*) and presence (*goniobathmos*) of an anterior lamella. These data suggest that the distinguishing mark between *Plectopylis* and *Chersaecia* cannot be the number of lamellae. I retain all species in the genus *Plectopylis* which has the two lamellae fuse at their upper ends, forming a structure which resembles the Greek letter lambda. All other former species of *Plectopylis* s.s. which has two independent lamellae are moved to the genus *Chersaecia*.

***Chersaecia feddeni* (Blanford 1865)**

Figure 7.36

- 1865 *Helix (Plectopylis) feddeni* Blanford, Journal of the Asiatic Society of Bengal, 34 (2): 75–76, 94. ["Prome", "Prome, close to the Pagoda"]
- 1868 *Helix feddeni*, — Pfeiffer, Monographia Heliceorum Viventium...: 398.
- 1875b *Helix (Plectopylis) feddeni*, — Godwin-Austen, Proceedings of the Zoological Society of London, 613, Plate 74, Fig. 7.
- 1875 *Helix (Plectopylis) Feddeni*, — Hanley & Theobald, Conchologia Indica (...): 52, Plate 131, Figs 1–3.
- 1878a *Helix (Plectopylis) fedden* (Sic!), — Nevill, Hand list of Mollusca in the Indian Museum: 71.
- 1887 *Helix (Plectopylis) feddeni*, — Tryon, Manual of Conchology (...): 163, Plate 35, Figs 84–87.
- 1889 *Helix (Plectopylis) Feddeni*, — Tapparone Canefri, Annali del Museo Civico di Storia Naturale di Genova, 2 (7): 323 (=47). ["Prome"]
- 1897k *Plectopylis feddeni*, — Gude, Science Gossip, 4: 171, Fig. 64.
- 1899d *Plectopylis feddeni*, — Gude, Science Gossip, 6: 75–77, Fig. 104.
- 1899e *Plectopylis (Plectopylis) feddeni*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Plectopylis) feddeni*, — Gude, Science Gossip, 6: 175.
- 1914b *Plectopylis (Plectopylis) feddeni*, — Gude, The Fauna of British India (...): 128–129, Fig. 63.

Under the name *Plectopylis leucochila* Gude 1897

- 1898a *Plectopylis leucochilus* Gude, Science Gossip, 4: 231, Fig. 66. ["Burma"].
- 1898b *Plectopylis leucochila*, — Gude, Science Gossip, 4: 264.
- 1898i *Plectopylis leucochilus*, — Gude, The Journal of Malacology, 7: 13–14, Fig. 9.
- 1899e *Plectopylis (Plectopylis) leucochila*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Plectopylis) leucochila*, — Gude, Science Gossip, 6: 175.
- 1914b *Plectopylis (Plectopylis) leucochila*, — Gude, The Fauna of British India (...): 126–127, Fig. 62.

Under the name *Plectopylis lissochlamys* Gude 1897

- 1897h *Plectopylis lissochlamys*, Gude, Science Gossip, 4: 70–71, Fig. 53. ["Burma"].
- 1898i *Plectopylis lissochlamys*, — Gude, The Journal of Malacology, 7: 11–13, Fig. 8.
- 1899e *Plectopylis (Plectopylis) lissochlamys*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Plectopylis) lissochlamys*, — Gude, Science Gossip, 6: 175.
- 1914b *Plectopylis (Plectopylis) lissochlamys*, — Gude, The Fauna of British India (...): 121–122, Fig. 59.

Under the name *Plectopylis magna* Gude 1897

- 1897h *Plectopylis magna*, Gude, Science Gossip, 4: 70, Fig. 52. ["Burma"].
1898i *Plectopylis magna*, — Gude, The Journal of Malacology, 7: 9–11, Fig. 7.
1899e *Plectopylis (Plectopylis) magna*, — Gude, Science Gossip, 6: 148.
1899f *Plectopylis (Plectopylis) magna*, — Gude, Science Gossip, 6: 175.
1914b *Plectopylis (Plectopylis) magna*, — Gude, The Fauna of British India (...): 122–123, Fig. 60.

Under the name *Plectopylis ponsonbyi* Godwin-Austen 1888

- 1888 *Helix (Plectopylis) ponsonbyi* Godwin-Austen, Proceedings of the Zoological Society of London, 243.
["Hlindet, Upper Burmah, 1500 feet"].
1894 *Plectopylis ponsonbyi*, — Pilsbry, Manual of Conchology (...): 155, Plate 40, Figs 9–12.
1896e *Plectopylis ponsonbyi*, — Gude, Science Gossip, 3: 178, Fig. 22.
1899e *Plectopylis (Plectopylis) ponsonbyi*, — Gude, Science Gossip, 6: 148.
1899f *Plectopylis (Plectopylis) ponsonbyi*, — Gude, Science Gossip, 6: 175.
1914b *Plectopylis (Plectopylis) ponsonbyi*, — Gude, The Fauna of British India (...): 119–120, Fig. 58.

Types: Prome-Pegu, NHMUK 1906.1.1.730 (3 syntypes of *feddeni*, two of them broken); Burma, NHMUK 1922.8.29.39 (holotype of *leucochila*); Burma, NHMUK 1922.8.29.38 (holotype of *lissochlamys*); Burma, NHMUK 1922.8.29.37 (holotype of *magna*); Burmah, Hlindet, NHMUK ??? (holotype of *ponsonbyi*); Burmah, coll. Godwin-Austen, NHMUK 1903.7.1.754/4 (probably syntypes of *pseudophis*);

Museum material examined: Burma, Mergui, coll. Dosch ex Rolle, SMF 172064/1 ("*magna*"); Barma, Prome, coll. Möllendorff, SMF 150099/1 ("*feddeni*"); Moulmein, coll. Möllendorff, SMF 150098/2 ("*lissochlamys*"); Moulmein, coll. Möllendorff, SMF 150095/1 (*ponsonbyi*); no locality, coll. Blanford, NHMUK/67; Ava (?), NHMUK/3; Pegu, Lower Burma, coll. Salisbury ex Beddome, NHMUK/1; India, Burmah, NHMUK 1871.9.23.205/3; India, Thyet Myo, NHMUK/2; Pegu, Thyet Myo?, coll. Blanford, NHMUK 1906.1.1.742/5; Burmah, NHMUK/3; Arakan Coast, Nioung jo, NHMUK 1888.12.4.1544–1547/4; no locality (from author), NHMUK 1888.12.4.1532/1; Burma, NHMUK/3; Burmah, NHMUK/6; Akouktoung, NHMUK 1888.12.4.1526–1528/3; Akouktoung, NHMUK/5; Burma, coll. Kennard ex Leipner ex Bullen, NHMUK/3; Burma, coll. Swinhoe, NHMUK/3; no data, coll. Blanford, NHMUK/3; Burma, NHMUK 1899.4.22.77/1 ("*lissochlamys*"); Tuonghoo, coll. Godwin-Austen ex Blanford, NHMUK 1923.2.15.5/2 ("*magna*"); Burma, Tonghu, leg. Theobald, coll. Blanford, NHMUK 1906.1.1.731/2 ("*magna*"); Burma, NHMUK 1899.4.22.78/1 ("*magna*");

Diagnosis: *Plectopylis feddeni* is a very variable species in terms of colour, spire height and in some aspects of the parietal plicae and lamellae. The forms assigned to this species agree in the following characters: protoconch matt, finely, rather irregularly wrinkled; callus slightly S-shaped; apertural fold free or almost free from the callus; there are two lamellae on the parietal wall which are not connected to each other; palatal plicae typical to the genus *Plectopylis*.

Differential diagnosis: See under *P. goniobathmos*.

Measurements (in mm): D= 16.1, H= 5.1 (syntype of *feddeni*); D= 25.4, H= 8.9 (holotype of *magna*); D= 16, H= 6.7 (holotype of *leucochila*); D= 17.8, H= 6 (holotype of *ponsonbyi*).

Distribution: The samples which are assigned to *Chersaecia feddeni* in this work has been collected exclusively from Burma (Myanmar). The southernmost known locality is Mergui and the other two known localities (Thyet Myo and Prome) are situated close to each other in Middle Myanmar (Bago and Mayway Regions) (Figure 7.124).

Remarks: Gude described nearly every single shell which slightly differed from the others under a different name. Even if some of the "species" handled here under the name *feddeni* differ from each other, there are no major outer shell characters which distinguish them.

The shell shape of *Plectopylis feddeni* is similar to that of *P. ponsonbyi*. The only difference is the reduced (short) main and lower plicae in the latter. In my understanding, this difference is insufficient to call these two forms under two different specific names. The single known shell of *P. ponsonbyi* could be the best explained by a *P. feddeni* specimen with reduced long plicae. Important to mention that Pilsbry (1894) and Gude (1896e) figured the plicae a specimen different form the type in the NHM, because the one I examined in the NHM was intact.

Plectopylis leucochila differs from the type of *P. feddeni* only by the elevated spire and therefore the domed dorsal surface. Otherwise, all plicae are similar. Although there are no available shells showing transitional character state in terms of spire height, this character is not sufficient to separate species.

The holotype of *P. lissochlamys* is very similar to that of *P. ponsonbyi*. The differences are the very slightly more elevated spire, the more descending aperture and the longer elongation of the right leg of *P. ponsonbyi*. The

holotype of *P. lissochlamys* has an apertural fold and a very low indication of the main plica between the anterior lamella and the apertural fold. This main plica may be better developed if the specimen lived longer. These shell characters are insufficient to call these specimens different species.

The holotype of *P. magna* differs from that of *P. lissochlamys* by the larger size, the long lower plica (which is present only under the lamellae in *P. lissochlamys*), and the longer anteriorly elongated lower part of the anterior lamella. All of these characters could be interpreted as intraspecific variability.

As a consequence, there is a continuous variation across the type specimens of *P. feddeni*, *P. lissochlamys*, *P. leucochila*, *P. magna* and *P. ponsonbyi* in terms of spire height, length of the main and lower plicae and the morphology of the anterior lamella. The available material does not allow seeing the geographic patterns of these variations. Available shell material suggests that handling all the above-mentioned taxa under the name *Plectopylis feddeni* would be the best solution until larger samples from exact localities become available.

***Chersaecia goniobathmos* (Ehrmann 1922)**

Figures 7.2, 7.39

1922 *Plectopylis* (*Plectopylis*) *goniobathmos* Ehrmann, Sitzungsberichte der naturforschender Gesellschaft zu Leipzig, 45–48: 10–12, Figs a–b; Fig. 3 on the plate. ["Pekon, südliche Shan-Staaten, in ca. 1000 m Höhe."].

Types: Süd. Schan-staten: Pekor, 1000 m, leg. W. Micholitz, coll. Ehrmann, SMF 150100a (lectotype); same data, SMF 150100b (paralectotype); same data, SMF 150100c (paralectotype); same data, SMF 150100d–e (2 paralectotypes).

Diagnosis: A sinistral, brownish, sinistral species with two lamellae, long main and lower plicae reaching the aperture. The 4th and 5th palatal plicae form a vertical ridge, the other plicae are horizontal, straight.

Description: Shell sinistral, flat or with slightly elevated spire; colour dark to light brown; protoconch very finely tuberculated, sometimes the tubercles are arranged in radial lines; teleoconch with reticulated structure with the radial sculpture being dominant; on the ventral side however, the spiral lines are of equal strength; the 6.25–6.75 (n=2) whorls are separated by rather shallow suture; whorls slightly angled, flat above; apertural margin reflexed and slightly thickened; parietal callus elevated, rather sharp and V-shaped, with two channels or furrows at the meeting point with the lip; apertural fold connected to the callus.

Two opened specimens were examined. Palatal wall with a rather straight posterior lamella with posteriorly elongated lower, and posteriorly as well as anteriorly elongated upper ends and a shorter, straight anterior lamella with posteriorly elongated upper and lower ends; the upper elongation of the anterior lamella does not reach the posterior lamella; main plica long, reaches the apertural fold without interruption; the main plica-apertural fold forms a long horizontal plica which is of equal height all along; intermediate plica short, lower plica very long, starts from below the posterior lamella and reaches the peristome. Palatal plicae are typical to that of the genus *Plectopylis*; first three plicae horizontal, straight, 4th and 5th form a vertical plate, and the last plica is also straight, horizontal, and very much elongate anteriorly.

Differential diagnosis: In general shell shape *P. goniobathmos* is similar to *P. leiophis*. There are however, considerable differences in the plication, namely (1) *P. leiophis* has only a single lamella (the anterior one is missing), whereas *P. goniobathmos* has two; (2) *P. goniobathmos* has a very long lower parietal plica, which is short in *P. leiophis*; (3) the palatal plica of *P. goniobathmos* are typical to that of the genus *Plectopylis*, but in case of *P. leiophis* the 4th and 5th plica do not form a vertical plate, but are oblique.

Plectopylis goniobathmos is probably the closest relative of *P. feddeni*, which is a very variable species. The main difference between the two species is that in *P. goniobathmos* the main plica connects the callus, whereas in *P. feddeni* they are independent.

Measurements (in mm): D= 14.7–16.4, H= 5.6–6.2 (n=3, holotype and syntypes).

Distribution: *Plectopylis goniobathmos* is known from the type locality only (Figure 7.124).

Chersaecia species1 u. sp.

Figure 7.37

Material: Burmah, Mogok, ruby mines, coll. Goodwin-Austen, 1 holotype.

Diagnosis: Shell large, flat, widely umbilicated, parietal wall with a single lamella and a short lower plica, palatal plicae oblique, with additional denticles at their posterior ends.

Description: Shell large, sinistral, almost completely flat, only the protoconch is a slightly elevated; original colour might be brownish-reddish; dorsal side of the protoconch irregularly, roughly wrinkled, but the ventral side (i.e. inside the umbilicus) is clearly tuberculated; the whole teleoconch irregularly wrinkled with sometimes signs of spiral lines (especially on the dorsal side); peristome very much thickened and slightly reflexed; callus well-developed, sharp, slightly S-shaped, with canals at both ends; apertural fold very short, denticle-like, free from the callus

Parietal wall with a single lamella and a short lower plica; palatal wall with six plicae, first and last straight, horizontal, remaining ones oblique, with additional denticles at their posterior ends.

Differential diagnosis: In size and shape it resembles to species of the genus *Plectopylis*. However, *Ch. species 1* u. sp. has straight, oblique palatal plicae, and a single lamella which differentiates it from all *Plectopylis* species, which have the 4th and 5th palatal plicae joined and form a vertical plate, and have two lamellae joined at their upper ends. The most similar *Chersaecia* species in outer shell morphology is *Ch. shanensis*, which nevertheless has well developed lower, main and middle plicae. All other *Chersaecia* species are much smaller and have well-developed main plicae.

Measurements (in mm): D= 23.6, H= 7.7 (holotype).

Type locality: Burmah, Mogok, ruby mines.

Distribution: The only specimen of *Chersaecia species 1* u. sp. is known from the type locality only (Figure 7.124).

Chersaecia perarcta (Blanford 1865)

Diagnosis: A small, flat species with a single lamella. Parietal plicae more or less straight, horizontal or oblique, sometimes with additional denticles.

Differential diagnosis: The most similar species is *Ch. perrieriae*, which has a longer middle plica and its 4th and 5th palatal plicae form a vertical plate. See also under *Ch. refuga*.

Chersaecia perarcta perarcta (Blanford 1865)

Figure 7.37

1865 *Helix (Plectopylis) perarcta* Blanford, Journal of the Asiatic Society of Bengal, 34 (2): 75, 94. ["Myaleit DOUNG, near Ava"].

1868 *Helix perarcta*, — Pfeiffer, Monographia Heliceorum Viventium...: 397.

1869 *Helix perarcta*, — Pfeiffer, Novitates conchologicae. Series prima...: 502, Plate 108, Figs 13–15.

1870 *Helix (Plectopylis) perarcta*, — Hanley & Theobald, Conchologia Indica (...): Plate 13, Fig. 3.

1875b *Helix (Plectopylis) perarcta*, Godwin-Austen, Proceedings of the Zoological Society of London, 613, Plate 74, Fig. 4.

1878a *Helix (Plectopylis) perarcta*, — Nevill, Hand list of Mollusca in the Indian Museum: 71.

1887 *Helix (Plectopylis) perarcta*, — Tryon, Manual of Conchology (...): 162, Plate 35, Figs 91–95.

1888 *Helix (Plectopylis) perarcta* Godwin-Austen, Proceedings of the Zoological Society of London, 243. ["Hlindet, 1200 feet"].

1896d *Plectopylis perarcta*, — Gude, Science Gossip, 3: 155, Fig. 19.

1899e *Plectopylis (Chersaecia) perarcta*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Chersaecia) perarcta*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Chersaecia) perarcta*, — Gude, The Fauna of British India (...): 106–108, Fig. 50.

Types: Myaleit doun, Ava, Burma, NHMUK 1906.2.2.275/6 (probably syntypes); Myaleit doun, near Ava, NHMUK 1888.12.4.1521–1523/3 probably syntypes.

Museum material examined: Burma, coll. Godwin-Austen ex Blanford, NHMUK 1909.3.15.61/3; Burma, Ava, coll. A. S. Kennard, NHMUK/1; Burma, Ava, NHMUK/3.

Diagnosis: Main plica present.

Description of the type series: Shell sinistral, closely coiled, flat, only the apex is elevated a bit; colour greyish yellow to light brown. Protoconch large (2.5–2.75 whorls) with large tubercles, no radial lines are visible; teleoconch with very fine ribs, which are covered by fine periostracal folds; spiral lines absent; the periostracum is more prominent within the sutures, probably because it can remain there more easily; the 5.75–6 whorls are separated by very deep suture; umbilicus regularly shaped infundibular, only the last whorl is widening abruptly; body whorl

rounded; apertural margin reflexed and slightly thickened; parietal callus is elevated, sharp and V-shaped, with two deep channels or furrows at the meeting point with the lip; the channels do not reach the penultimate whorl.

Two specimens were opened. Parietal wall with a single, well-developed lamella which has the lower end elongated slightly posteriorly; upper end both anteriorly and posteriorly very slightly elongated; main plica long, free from the lamella, reaches the callus; one of the shells had the main plica and the apertural fold separated (probably subadult shells); the inner end of the main plica is situated lower (closer to the lower suture); lower plica slender, runs along and parallel with the lower suture and also reaches the callus; there is a very short additional plica between the main and the lower plica; all plica start in one vertical line anterior to the lamella; palatal plicae 6, first and 6th straight, run parallel with the sutures; the middle plicae are more or less horizontal, straight or slightly wavy; sometimes with additional posterior denticle.

Differential diagnosis: See under *Chersaecia perarcta simplex*.

Measurements (in mm): D= 10.6–11.7, H= 3.6–4.1 (n=3, type series, NHMUK 275.06.2.2).

Distribution: *Chersaecia perarcta perarcta* was reported only from the vicinity of Ava, Mandalay Region, Myanmar (Figure 7.124).

Chersaecia perarcta simplex (Solem 1966)

1966 *Plectopylis* (*Chersaecia*) *simplex* Solem, *Spolia Zoologica Musei Hauniensis*, 23: 97–101. Figs 23 c–g, 24, Plate 3, Figs a–c. ["Chieng Dao, North Thailand at 1,200–1,300 meters elevation"].

Types: Chieng Dao, 1200–1700 m O. H., N. Thailand, leg. Degerbøl (nr. 979), 1.7.1960, S.E. Asien, ZMUC-GAS-487 (2 broken specimens in ethanol + 1 intact shell).

Diagnosis: Main plica absent.

Differential diagnosis: The shell shape of *Chersaecia perarcta* and *Plectopylis simplex* do not differ. The nominotypical subspecies has, but the *Ch. perarcta simplex* lacks the main plica.

Measurements (in mm): D= 12.6, H= 4.1 (n=1, ZMUC-GAS-487).

Characters of the genital system (Solem 1966): Hermaphroditic duct a straight tube to middle of albumen gland, to large carrefour. Talon a slender, sinuated stark white duct along side of upper broadened hermaphroditic duct area. Carrefour with a solidified internal calcareous mass, opening into sharply differentiated prostate and uterus. Prostate enlarged below head portion, wide, becoming narrower and thinner where brood portions of uterus expands. Upper third of uterus slender, lower two-thirds grossly expanded with well-developed embryos. Vas deferens an irregularly coiled tube passing along vagina to penioviducal angle. There it becomes an integral part of the fibres surrounding the penis, ascends penis laterally to its head, entering through small penis papilla. No epiphallic differentiation observed. Penis a relatively short muscular tube with a thick apical retractor muscle attaching to diaphragm. Internally, penis with about eight corrugated longitudinal pilasters, those situated next to the vas deferens distinctly larger. At apex of penis two large pilasters flank a small vergic papilla with basal epiphallic pore. Gonopore located behind and below left tentacle. atrium extremely short. Free oviduct very short, only slightly narrowed from base of uterus. Spermatheca with very long slender stalk and a pendulous enlarged head lying above broadened area of uterus with tip of head nearly reaching carrefour. Vagina very long, upper part broad and stuffed with gelatinous tissue. Several sheets of muscle fibres bind atrial and vaginal areas to body wall.

Distribution: *Chersaecia perarcta simplex* is known from the type locality only (Figure 7.124).

Remarks: Because of the similar (indistinguishable) shells, *Plectopylis* (*Chersaecia*) *simplex* is handled as a subspecies of *Ch. perarcta*. The difference between the two forms is only the presence/absence of the main plica. See also remarks under *Ch. refuga*.

Chersaecia perrieriae (Gude 1898)

Figure 7.39, 7.98

1898a *Plectopylis perrieriae* Gude, *Science Gossip*, 4: 231–232, Fig. 67. ["Thayet-Mayo, Pegu, Burma"].

1898i *Plectopylis perrieriae*, — Gude, *The Journal of Malacology*, 7: 14–16, Fig. 10.

1899e *Plectopylis* (*Chersaecia*) *perrieriae*, — Gude, *Science Gossip*, 6: 148.

1899f *Plectopylis* (*Chersaecia*) *perrieriae*, — Gude, *Science Gossip*, 6: 175.

1914b *Plectopylis* (*Chersaecia*) *perrieriae*, — Gude, *The Fauna of British India* (...): 103–105, Fig. 48.

Types: Pegu, ex coll. Linter, NHMUK 1922.8.29.40 (holotype).

Museum material examined: Kyengdwen valley, Burmah, leg Ogle, coll. Godwin-Austen, NHMUK 1903.7.1.776/2.

New material examined: 2009.10.19A Myanmar, Shan, Pindaya, Pindaya Cave 20°55.409'N, 96°39.038'E, alt. 1294 m, Leg.: K. Ohara, et al. 19.10.2009.

Description of the type series: The holotype and two additional shells are from different samples. They differ only in size, therefore the description is based on these three shells. The differences between the three shells and the sample 2009.10.19A are written under the remarks part.

Shell sinistral, almost entirely flat, only the apex is elevated a bit; all three specimens were corroded therefore the original colour could not be examined; protoconch finely tuberculated, and the last whorl is irregularly, roughly wrinkled; teleoconch finely reticulated on the dorsal side, elsewhere ribs are the dominant (the holotype is reticulated everywhere); the 6–6.5 whorls (n=3) are separated by rather shallow (holotype) or moderately deep (other 2 shells) suture; body whorl rounded but angulated above (upper part flat); apertural margin slightly thickened and very slightly reflexed; parietal callus is elevated, sharp and V-shaped, the upper branch of the V being shorter; there are two shallow channels or furrows at the meeting point of the callus and the peristome; the channels do not reach the penultimate whorl.

Two specimens were opened (the holotype and one shell from the other sample). Parietal wall with a single, well-developed, curved lamella with posteriorly elongated lower part; main plica long, free from the lamella, its posterior end is situated above the middle point of the lamella, than anteriorly runs a bit lower, reaching the middle line of the lamella, and runs up (closer to the upper suture) again; lower plica very slender, starts under the lamella and reaches the peristome, but is interrupted in the middle. Palatal plicae 6, the first is, second and third are straight and horizontal or slightly oblique, the fourth and fifth form a vertical plate which has a bifurcated lower end; the sixth plica is very long and divided, its anterior end is much longer.

Differential diagnosis: *Ch. perrieriae* differs from *Ch. leiophis* by the long lower plica which reaches the peristome (this is very short in *leiophis*) and the main plica which is straight in *Ch. leiophis*, but curved in *Ch. perrieriae* (see description).

Measurements (in mm): D= 14.8, H= 5.9 (holotype); D= 11.1–11.95, H=3.8–5.2 (n= 3, 2009.10.19A); D= 12.6–12.9, H= 4.5–4.7 (n=2, NHMUK 776.03.VII.1).

Characters of the genital structure: One specimen was anatomically examined. Locality information: 2009.10.19A Myanmar, Shan, Pindaya, Pindaya Cave 20°55.409'N, 96°39.038'E, alt. 1294 m, Leg.: K. Ohara, et al. 19.10.2009.

Left ommatophoral retractor passes between penis and vagina. Atrium very short; penis long, slender, cylindrical; internally with 3 longitudinal folds; epiphallus not found, vas deferens originates from the penis wall approximately at the middle of the penis; retractor muscle insert on the distal end of the penis, as thick as the penis and slightly shorter; it attaches on the diaphragm; vas deference becomes gradually free from leaving the middle part of the penis, after the curved part of the vagina it is entirely free, before that it runs together with the vagina and attached to it with weak fibres; at its terminal part the vas deferens is very much thickened, even thicker than the penis; vagina cylindrical, a little flattened close to the atrium; it is slightly longer than the penis and about 2–3 times thicker; several, slender muscle fibres attach the vagina to the body wall; pedunculus short, spermoviductus well-developed, uterus with four large embryos; gametolytic sac is approx. two times longer than the diverticulum; diverticulum relatively thick at its entire length, but the stalk of the gametolytic sac is slender, and the gametolytic sac itself is slightly thickened (reaching the thickness of the diverticulum); both organs originate near the point where the vas deferens joins the pedunculus; talon slender, relatively long.

Radula: Figure 7.98 and Table 7.4.

Distribution: The only known locality is Thyet Myo in Magway Region, Myanmar. A newly collected sample resembling typical *Ch. perrieriae* (see Remarks) has been collected in the eastern part of Shan Region (Figure 7.124).

Remarks: The newly collected sample from Myanmar (2009.10.19A) provided information addition to the old museum specimens. The shell colour is reddish brown, and the protoconch is finely tuberculated. The shells belonging to this sample are overall smaller and flatter than others described above and have more angulated body whorls. The main plica "curves down" in the direction of the intermediate plica and there the distance between them is very small. This area between the two plicae can be covered with white calcium layer, which can be homologous with the anterior lamella of *Plectopylis* species.

The shell shape of the newly collected specimens somewhat resembles to the nearby occurring *Chersaecia woodthorpei*, however that species has two lamellae and three short, parallel, straight palatal plicae next to the vertical plate which is formed by the 4th and 5th plicae.

Chersaecia refuga (Gould 1846)

Diagnosis: A very variable species with single lamella and usually oblique palatal plicae.

Differential diagnosis: *Chersaecia perarcta* is smaller and flatter, usually with concave surface. *Ch. feddeni* has two lamellae. See also under *Ch. goniobathmos*.

***Chersaecia refuga refuga* (Gould 1846)**

Figures 7.2, 7.38

Under the name *refuga*

1846 *Helix refuga* Gould, Proceedings of the Boston Society of Natural History, 2, 99. ["Tavoy"]

1847 *Helix refuga*, — Philippi, Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien: 52, Plate 10, Fig. 4.

1847 *Helix refuga*, — Philippi: Abbildungen und Beschreibungen...: 3: 2–3, Plate 10, Fig. 4. ["imperium Birmanorum Indiae orientalis"].

1848 *Helix refuga*, — Pfeiffer, Mart. & Chemnitz: 1(12): 367, pl. 64, Figs 19–21.

1850 *Helix (Atopa) refuga*, — Albers, Die Heliceen...: 90.

1854 *Helix refuga*, — Reeve: Conchologia Iconica, Vol 7, species 436, Plate 82, Fig. 436, 436 a–b.

1855 *Helix (Corilla) refuga*, — Adams, H. & Adams, A., The genera of recent Mollusca...: 208.

1857 *Helix refuga*, — Theobald, Journal of the Asiatic Society of Bengal, 26: 249.

1862 *Helix (Corilla) refuga*, — Gould, Otia Conchologica...: 198.

1868 *Helix refuga*, — Pfeiffer, Monographia Heliceorum Viventium...: 396.

1870 *Helix (Plectopylis) refuga*, — Hanley & Theobald, Conchologia Indica (...): 7, Plate 13, Fig. 9.

1875a *Helix (Plectopylis) refuga* (synonym of *leiophis*), — Godwin-Austen, Proceedings of the Zoological Society of London: 44.

1878a *Helix (Plectopylis) refuga*, — Nevill, Hand list of Mollusca in the Indian Museum: 71.

1887 *Helix (Plectopylis) refuga*, — Tryon, Manual of Conchology (...): 164, Plate 35, Fig. 1.

1899c *Plectopylis refuga*, — Gude, Science Gossip, 6: 15, Fig. 75.

1899c *Plectopylis refuga*, — Gude, Science Gossip, 6: 16–17.

1899e *Plectopylis (Chersaecia) refuga*, — Gude, Science Gossip, 6: 148.

1899e *Plectopylis (Chersaecia) refuga*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Chersaecia) refuga*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Chersaecia) refuga*, — Gude, The Fauna of British India (...): 102–103, Fig. 47.

1964 *Plectopylis (Plectopylis) refuga*, — Johnson, The recent Mollusca of Augustus Addison Gould: 139, Plate 38, Fig. 9.

Under the name *leiophis* Benson 1860

1860a *Plectopylis Leiophis*, Benson, Annals and Magazine of Natural History, 3 (5): 244, 246. [ad Kwadouk, prope Thyet Mio].

1865 *Helix (Plectopylis) leiophis*, — Blanford, Journal of the Asiatic Society of Bengal, 34 (2): 94. ["Thyett Myo", "Akoutoung"]

1868 *Helix leiophis*, — Pfeiffer, Monographia Heliceorum Viventium...: 396.

1870 *Helix (Plectopylis) leiophis*, — Hanley & Theobald, Conchologia Indica (...): Plate 13, Fig. 8.

1875b *Helix (Plectopylis) leiophis*, Godwin-Austen, Proceedings of the Zoological Society of London, 610–612, 613, Plate 74, Fig. 2.

1875a *P. leiophis* (synonym of *refuga*), — Godwin-Austen, Proceedings of the Zoological Society of London, 44.

1887 *Helix (Plectopylis) leiophis*, — Tryon, Manual of Conchology (...): 163, Plate 35, Figs 88–89.

1899c *Plectopylis leiophis*, — Gude, Science Gossip, 6: 16, Fig. 76.

1899e *Plectopylis (Chersaecia) leiophis*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Chersaecia) leiophis*, — Gude, Science Gossip, 6: 175.

1908a *Plectopylis (Chersaecia) leiophis*, — Gude, Proceedings of the Malacological Society of London, 8: 88–89.

1914b *Plectopylis (Chersaecia) leiophis*, — Gude, The Fauna of British India (...): 99–102, Figs 44–46.

1960 *Plectopylis (Chersaecia) leiophis*, — Zilch, Handbuch der Paläozoologie...: 595., Fig. 2093.

Under the name *pseudophis* Godwin-Austen 1875

- 1875a *Plectopylis pseudophis*, — Godwin-Austen, Proceedings of the Zoological Society of London, 44. ["Thayatmyo, in Pegu"].
- 1875b *Helix (Plectopylis) pseudophis*, Godwin-Austen, Proceedings of the Zoological Society of London, 610–612, 613, Plate 74, Fig. 3.
- 1887 *Helix (Plectopylis) pseudophis*, — Tryon, Manual of Conchology (...): 162, Plate 35, Figs 80, 81.
- 1897k *Plectopylis pseudophis*, — Gude, Science Gossip, 4: 170, Fig. 62.
- 1899c *Plectopylis pseudophis*, — Gude, Science Gossip, 6: 17, Fig. 77.
- 1899e *Plectopylis (Chersaecia) pseudophis*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Chersaecia) pseudophis*, — Gude, Science Gossip, 6: 175.
- 1908a *Plectopylis (Chersaecia) pseudophis* (synonym of *leiophis*), — Gude, Proceedings of the Malacological Society of London, 8: 88–89.

Under the name *kengtungensis* Gude 1914

- 1914a *Plectopylis (Chersaecia) kengtungensis* Gude, Proceedings of the Malacological Society of London. 11 (1): 53 (+ unnumbered figure). [E. Burma: Kengtung].
- 1914b *Plectopylis (Chersaecia) kengtungensis*, — Gude, The Fauna of British India (...): 97–98, Fig. 43.

Under the name *nagaensis* Godwin-Austen 1875b

- 1875b *Helix (Plectopylis) nagaensis*, Godwin-Austen, Proceedings of the Zoological Society of London, 609–610, 612, Plate 73, Fig. 4. ["Prowi, head of the Lauier river, Nágá hills, 5000 feet"].
- 1878a *Helix (Plectopylis) nagaensis*, — Nevill, Hand list of Mollusca in the Indian Museum: 72.
- 1887 *Helix (Plectopylis) nagaensis*, — Tryon, Manual of Conchology (...): 161, Plate 35, Figs 78, 79.
- 1897a *Plectopylis nagaensis*, — Gude, Science Gossip, 3: 206–207, Fig. 33.
- 1899e *Plectopylis (Chersaecia) nagaensis*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Chersaecia) nagaensis*, — Gude, Science Gossip, 6: 175.
- 1914a *Plectopylis (Chersaecia) nagaensis*, — Gude, Proceedings of the Malacological Society of London. 11 (1): 54.
- 1914b *Plectopylis (Chersaecia) nagaensis*, — Gude, The Fauna of British India (...): 96–97, Fig. 42.

Under the name *degerbolae* Solem 1966

- 1966 *Plectopylis (Chersaecia) degerbolae* Solem **new synonym**, *Spolia Zoologica Musei Haumiensis*, 24, 95–97. Figs 23 a–b., Plate 2, Figs F–H. ["Doi Sutep, North Thailand at 1,000 meters elevation (number 1173)"].

Types: Burmah, Shan States, NHMUK 1903.7.1.750 (3 syntypes of *kengtungensis*); Naga Hills, Prowi, head of Lanier valley, coll. Godwin-Austen, NHMUK 1903.7.1.753/10 (syntypes of "*nagaensis*"); Tavoy, British Burma, MCZ 169335 (lectotype of *refuga*); Tavoy, Burma, coll. Gould, MCZ 87871 (paralectotype of *refuga*); Doi Sutep, 1000 m O. H., N. Thailand, leg. Degerbøl (nr. 1173), 1.7.1960, ZMUC-GAS-485.

Museum material examined: Pegu, NHMSB 122178/1; no locality data (alte Schau-Slg.), SMF 150114/1; no locality data (alte Schau-Slg.), SMF 150116/1 ("*refuga*"); Barma, coll. Möllendorff, photographed for Zilch (1960), SMF 150115/3; Brit. Indien, coll. Dosch ex Rolle (Schlüter), SMF 172055/1; Naga Hills, NHMUK/2 ("*nagaensis*"); India, coll. Godwin-Austen, NHMUK 1909.3.26.74/2 ("*nagaensis*"); India, Naga Hills, NHMUK 1891.3.17.352/1 ("*nagaensis*"); NE Manipur, Prowi, coll. Godwin-Austen, NHMUK/9 ("*nagaensis*"); Naga Hills, leg. Ogle, coll. Godwin-Austen, NHMUK/1 ("*nagaensis*").

Diagnosis: Main plica present.

Description of typical *leiophis*: Shell sinistral, flat above or with very slightly elevated spire; colour light brown to yellowish and white; protoconch very finely tuberculated, and some shells (e.g. the two from "Burma, small, type, m. c.") has very fine wrinkles all over the tuberculated protoconch, whereas others (e.g. third shell from the same sample) are not wrinkled at all, only tuberculated; teleoconch with reticular structure, only the basal part of the body whorl (periumbilical region) is smooth; on the dorsal surface and inside the umbilicus the spiral lines are dominant, or the spiral and the radial lines are of the same strength, whereas on the edge of the body whorl spiral lines are not visible; the 5.75–6.25 (n=3) whorls are separated by rather shallow suture; whorls angled, flat above; apertural margin slightly reflexed and slightly thickened; parietal callus elevated, rather sharp and V-shaped, with two channels or furrows at the meeting point with the lip; the channels do not reach the penultimate whorl; apertural fold connected to the callus.

Three opened specimens of typical *leiophis* were observed in the NHMUK. Plication is very variable. Palatal wall with a single curved lamella and a long main plica reaching the apertural fold; one opened shell had a lower and

a middle plica; the second shell had a lower plica, a middle plica and an intermediate plica, whereas the third shell had the main plica very short and the middle plica also vestigial. Palatal plicae six or seven, first and last plicae are straight, the middle ones are straight, horizontal, or oblique, or sometimes even the 4th and 5th are vertical; sometimes the plicae have a posterior denticle.

Differential diagnosis: See under *Ch. refuga muspratti*.

Measurements (in mm): D= 14.55–15.3, H= 6.1–6.9 (n= 3, NHMUK 88.12.4.1526–28, typical *leiophis*); D= 11.6–12.2, H= 6.3–6.8 (n=3, type series of *nagaensis*); D=16.2, H= 6.2 (n=1, paratype of *degerbolae*, ZMUC-GAS-485)

Distribution: The samples assigned to *Chersaecia refuga* in this study have been collected from a wide area from the Indian Nagaland to Southern Myanmar (Figure 7.124).

Remarks: Gude (1899c) was unable to loan the type specimen of *Plectopylis refuga*, and received only drawings and photos from the curator of the New York State Museum. The drawings of Dr. Merrill show one or two specimens, which were opened in order to show the parietal plicae and lamellae. I loaned the lectotype of *Plectopylis refuga* (MCZ 169335) and received photos of two samples of paralectotypes (MCZ 87871, MCZ 142866). The sample MCZ 87871 contains a single shell which is very similar to the paralectotype. The other sample (MCZ 142866) contains five shells, which probably belong to a different species (possibly *Chersaecia feddeni*) because they have rounded body whorls whereas *P. refuga* has shouldered one. None of the above-mentioned shells are open to show the parietal plicae. Thus, it is unclear which shells were examined and figured by Dr. Merrill. Both the lectotype (MCZ 169335) and the similar paralectotype (MCZ 87871) have a small hole on the shell ca. half way between the armature and the aperture. This hole does not allow careful examination of the parietal lamella and the adjacent plicae. The only thing is visible that there is main plica starting from the peristome, but it gets lower and gradually weakens and disappears in the direction of the lamella. Loer plica not visible. The palatal plicae are short and rather horizontal; the 5th is thick and vertical with a short horizontal posterior denticle. The shell shape of the two syntypes of *refuga* and typical *leiophis* are similar. The only diagnosable difference is the presence of a lower plica in *P. leiophis* and the absence of that plica in *P. refuga*. The parietal plication of typical *leiophis* specimens is very variable. At the moment I see no reason to separate them on species level based on this single trait. I refer to *Plectopylis leiophis* as the synonym of *Plectopylis refuga*.

The relationship between *Plectopylis pseudophis* and *P. leiophis* was discussed by Gude (1908a). According to him, the typical forms differ in the following characters: tooth outline of the lamella, elevated spire and the absence of a short horizontal parietal plica between the main and intermediate plicae in *pseudophis*, and the smooth lamella, flat spire and the presence of that additional plica between the main and intermediate plicae in *leiophis*. Based on the specimens examined by Gude (1908a) these characters are all unstable, and provide no separation of two species. Therefore *Plectopylis pseudophis* has been handled as the synonym of *P. leiophis*.

Plectopylis kengtungensis was compared only with *P. nagaensis* and *P. muspratti* in the original description. Gude (1914a) have not compared *P. kengtungensis* with *P. leiophis*, probably because he was strongly relying on the morphology of the palatal plicae in his classification. According to the original description of *P. kengtungensis*, it has the palatal plicae united with a "low transverse ridge", whereas this has not been mentioned in the case of *P. leiophis*. This character, however, varies considerably between specimens probably depending on their age. Older shells tend to have more calcium layers laid on both the parietal and palatal sides of the armature. Regardless of the ridge, the morphology of palatal plicae of typical *kengtungensis* and *leiophis* are similar (usually long plicae with small denticles posteriorly, and the 5th plica is oblique). The parietal plicae and lamellae also show no considerable differences between *kengtungensis* and *leiophis*. The shell shape of typical *leiophis* is quite flat, whereas the spire of *P. kengtungensis* is slightly elevated. This character is also not reliable, because the typical *pseudophis* (= synonym of *leiophis*) form, has similar shell shape to that of *P. kengtungensis*. Because of the above-mentioned information, I synonymise *Plectopylis kengtungensis* with *P. leiophis*.

Typical *Plectopylis leiophis* shells are entirely flat, have angulated body whorl, and have a relatively long middle plica, joined to the lamella, whereas the typical *P. nagaensis* shells have domed apical side with rounded body whorl and their middle plica is missing. These differences are, however, not stable across populations. The shells described as *Plectopylis pseudophis* have somewhat elevated spire, and with this, form connection between the flat *leiophis* and the domed *nagaensis*. One shell of the type series of *P. nagaensis* which was opened probably by the author of the species, had a denticle-like plica in some distance from the lamella in anterior direction, in the line of the middle plica. The same vestigial plica was visible in another sample ("India", NHMUK 74.9.26.3). These show that the middle plica of *Plectopylis nagaensis* is not missing in all specimens, but sometimes present in a vestigial form. Because of these observations I synonymize *Plectopylis nagaensis* with *P. leiophis*. The "dwarfed variety" of *Plectopylis nagaensis*, which was mentioned in the original description of the species, is described under the name *Chersaecia shiroiensis* subspecies 1.

Plectopylis (Chersaecia) degerbolae do not differ in shape from typical *P. leiophis* specimens. The diagnosable difference is the presence (*leiophis*) and absence (*degerbolae*) of the lower plica. At the moment I do not find it supported to distinguish two species on the basis of this single trait. More material from more exact localities are needed to examine the stability of this, and other shell characters. Here I refer to *P. degerbolae* as the synonym of *Chersaecia refuga*.

According to the original descriptions of *P. degerbolae* and *P. simplex*, the protoconchs are with "irregular growth wrinkles" and are "smooth", respectively. I examined paratype specimens of both species and found that both species have very finely tuberculated protoconchs. This trait is characteristic of the genus. Addition to the tubercles, the second whorl of the protoconch is irregularly wrinkled in the paratype of *P. degerbolae*, but no wrinkles were found on the protoconch of the paratype of *P. simplex*.

***Chersaecia refuga muspratti* (Gude 1897)**

Figure 7.38

1897f *Plectopylis muspratti* Gude, Science Gossip, 4: 10, Fig. 45. [Naga Hills, Assam].

1898i *Plectopylis muspratti*, — Gude, The Journal of Malacology, 7: 7–8, Fig. 5.

1899e *Plectopylis (Chersaecia) muspratti*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Chersaecia) muspratti*, — Gude, Science Gossip, 6: 175.

1914a *Plectopylis (Chersaecia) muspratti*, — Gude, Proceedings of the Malacological Society of London. 11 (1): 54.

1914b *Plectopylis (Chersaecia) muspratti*, — Gude, The Fauna of British India (...): 89–90, Fig. 43.

Types: Naga Hills, coll. Beddome, NHMUK 1912.4.16.320 (holotype).

Diagnosis: A subspecies of *Chersaecia refuga* which lacks the main plica.

Description: The description of the outer shells characters is based on the two syntypes deposited in the NHM. No additional material found in the collection. Gude (1897f) described and figured the inner plicae based on the shells in Colonel Beddome's collection. I copy his description here.

Shell sinistral, with elevated spire, upper side conical; one of the shells is corroded, but the other has yellowish grey basic colour with reddish stripes; this results in a mosaic-like coloration on the dorsal side; protoconch matt, almost smooth or with irregular growth lines; teleoconch with fine reticular structure; the 6–6.5 (n=2) whorls are separated by rather suture; whorls rounded, not angled; peristome reflexed and slightly thickened, callus normally developed, S-shaped, with canals at both ends at the meeting points with the peristome; apertural fold shorter than the callus, connected to it.

Differential diagnosis: *Ch. refuga muspratti* differs from the domed-shelled populations of the nominotypical subspecies (typical *nagaensis* and *pseudophis*) by the absence of the main plica.

Measurements (in mm): D= 11.7–12.9, H= 6.6–6.75 (syntypes, n= 2).

Distribution: The subspecies is known from the type locality only (Figure 7.124).

Remarks: The only notable difference between *Plectopylis muspratti* and typical *Plectopylis nagaensis* (synonym of *P. refuga*) is the presence (*nagaensis*) and the absence (*muspratti*) of the main plica. Since there is no difference in the general shell and aperture shape, I refer to *P. muspratti* as a subspecies of *P. refuga*.

***Chersaecia shanensis* (Stoliczka 1873)**

Figures 7.2, 7.29, 7.37, 7.53, 7.93, 7.96, 7.98

Under the name *shanensis*

1873 *Plectopylis shanensis* Stoliczka, *Journal of the Asiatic Society of Bengal*, 42 (2), 170. [Provinciam Burmanam 'Shan-states' dictam].

1875 *Helix (Plectopylis) shanensis*, — Hanley & Theobald, *Conchologia Indica...*: Plate 149, Figs 8–9.

1878a *Helix (Plectopylis) shawensis* (sic!), — Nevill, Hand list of Mollusca in the Indian Museum: 71.

1887 *Helix (Plectopylis) shanensis*, — Tryon, Manual of Conchology (...): 162, Plate 36, Figs 10–11.

1897g *Plectopylis shanensis*, — Gude, Science Gossip, 4: 36, Fig. 48.

1899d *Plectopylis shanensis*, — Gude, Science Gossip, 6: 77, Fig. 105.

1899e *Plectopylis (Chersaecia) shanensis*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Chersaecia) shanensis*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Chersaecia) shanensis*, — Gude, The Fauna of British India (...): 111–112, Fig. 53.

1920 *Plectopylis (Chersaecia) shanensis*, — Gude, Journal of Molluscan Studies, 14 (2–3): 62–63.

Under the name *trilamellaris*

1875a *Helix (Plectopylis) trilamellaris* Godwin-Austen, Proceedings of the Zoological Society of London, 43–44. [Burmah. Exact locality unknown]

1878a *Helix (Plectopylis) trilamellaris* (synonym of *shawensis* sic!), — Nevill, Hand list of Mollusca in the Indian Museum: 71.

1879a *Helix (Plectopylis) trilamellaris* (synonym of *shanensis*), — Godwin-Austen, Journal of the Asiatic Society of Bengal, 48 (2): 2.

Types: According to Godwin-Austen (1879a), the collection of Stoliczka was deposited in the Indian Museum (today: Zoological Survey of India). ZSI do not loan specimens. In the case another species (*Endothyrella aborensis*, see also there) I received low quality photos, which did not help in confirming the identity of those shells. Therefore, in case of *P. shanensis*, I have not asked the curator of the ZSI for help. According to Godwin-Austen (1879a), G. Nevill compared his *Plectopylis trilamellaris* with Stoliczka's type specimens of *P. shanensis*, and he confirmed their identity. According to the original description of *P. trilamellaris*, two specimens (syntypes) are present in the collection of the Indian Museum, Calcutta.

Museum material examined: Shan States, NHMUK 1906.1.1.736/1; Shan States, NHMUK 1888.12.4.1551–1552/2.

New material examined: Myanmar, Mandalay, near Yinmabin Vill., 289 m, 20°49.540'N 96°24.830'E, leg. Ohara, K., 18.10.2009, PGB/5; Myanmar, Shan, Kalaw, Shwe U Min Cave, 1340 m, 20°37.256'N 96°33.443'E, leg. Ohara, K., 18.10.2009., PGB/3; Myanmar, Shan, in the suburbs of Kalaw, Myin Mahti Cave, 1320 m, 20°35.417'N 96°36.720'E, leg. Ohara, K., 18.10.2009., PGB/4.

Diagnosis: A sinistral, medium-sized, brownish-corneous species with long upper and lower horizontal plicae on the parietal wall, which run up to the aperture. A shorter middle plica is usually visible from the aperture. Palatal plicae are parallel and straight, sometimes divided.

Description: The sinistral, shiny, brownish-corneous or reddish shell is flat, with only the apex rising above the planar dorsal surface. The granulated surface is also visible on the ventral surface of the protoconch (umbilical view). The teleoconch is finely, irregularly wrinkled, consisting of 6.5–7 whorls. The umbilicus is very wide and moderately deep. The white apertural margin is reflexed and slightly thickened. The parietal callus is elevated, sharp and V-shaped, with two deep channels or furrows at the meeting point with the lip.

Four specimens were opened. On the parietal wall there is a single, short, vertical lamella with posteriorly slightly elongated upper and lower ends. At the lower angle of the lamella, a short horizontal plica is attached, its length is variable and it is sometimes visible through the aperture. In some shells (subadults?), this middle plica is free from the lamella. The upper and lower horizontal plica are not connected to the lamella and run all the way to the apertural margin. On the palatal wall there are usually seven horizontal, straight plicae. The first is short and runs parallel with the suture, the second is the longest, and the remaining ones are of the same length. Shorter plicae are visible posteriorly of the seven horizontal plicae with usually more than one denticle-like plica belongs to one long plica.

Differential diagnosis: The large, reddish-brownish shell, the lower and main plica which reun until the peristome, the long intermediate plicae and the horizontal palatal plicae are characteristic of this species and allows separation from all congeners. See also under *Ch. species1* u. sp.

Measurements (in mm): D= 19.1–20.1 H= 6.9–7.4 (2009.10.18B, n=2); D= 14.4–15.5, H= 5–5.4 (2009.10.18C, n=2).

Characters of the genital structure: Two specimens were anatomically examined. "Specimen1" had no embryos in its uterus, locality information: Myanmar, Shan, Kalaw, Shwe U Min Cave, 1340 m, 20°37.256'N 96°33.443'E, leg. Ohara, K. et al., 18.10.2009.; "Specimen2" had approximately 7 embryos in its uterus, locality information: Myanmar, Shan, in the suburbs of Kalaw, Myin Mahti Cave, 1320 m, 20°35.417'N 96°36.720'E, leg. Ohara, K., 18.10.2009., PGB/4.

The left ommatophoral retractor crosses the genitalia. Penis very long, cylindrical, in "Specimen1" internally with approximately 10 irregular longitudinal folds which are interrupted into squamous particles, in "Specimen2" the longitudinal folds are hardly recognisable, the inner penial surface is rather irregularly wrinkled, squamous; epiphallus slightly shorter than the penis, although the boundary between the epiphallus and vas deferens is not clearly visible; inter wall of the epiphallus with fine tubercles; epiphallus slightly wavy, especially shortly after its insertion to the penis; this wavy structure is stronger in "Specimen2" than in "Specimen1"; the extremely long retractor muscle attaches at the end of a very short penial caecum (see also discussion on the presence/absence of a

penial caecum); vas deferens slender, cylindrical, runs along the vagina and becomes thickened and curly near its insertion to the spermoviductus; vagina extremely long; gametolytic sac longer than the diverticulum, it has with slightly thickened gametolytic sac, whereas the diverticulum is almost equally thin towards the end.

Radula: Figure 7.98 and Table 7.4.

Distribution: Three precise localities are known for this species on the border of Mandalay and Shan provinces (Figure 7.124).

Remarks: The species is very variable in its shell characters. The population from the Shwe U Min Cave is identical with the specimens in the NHMUK. The shells from the other two localities are much smaller and usually have shorter middle plica on the parietal wall. Some specimens from Yinmabin Village have only straight palatal plicae without small plicae posteriorly.

Chersaecia shiroiensis (Godwin-Austen 1875b)

Diagnosis: Shell small, last quarter of whorl keeled on the basal side having a shallow groove between the suture and the keel; main parietal plica long, its posterior portion is much more elevated than the anterior, and bends downwards (in the direction of the lower suture). 4th and 5th palatal plicae are vertical in *Chersaecia shiroiensis shiroiensis*, but this trait could not be observed in the other subspecies. The last (6th) plica ends very close to the peristome, and visible from oblique view from the aperture.

Differential diagnosis: The shape of the last half/quarter of whorl (groove and periumbilical keel) is characteristic of this species. See also under both subspecies.

Remarks: The two subspecies differ considerably in the parietal plication, but they are almost identical in outer shell characters, therefore they are handled as subspecies of a single species.

Chersaecia shiroiensis shiroiensis (Godwin-Austen 1875b)

Figure 7.37

1875b *Helix* (*Plectopylis*) *shiroiensis*, Godwin-Austen, Proceedings of the Zoological Society of London, 609, 613, Plate 73, Fig. 3. ["slopes of the peak of Shiroifurar, N.E. of Manipur, at an altitude of from 8000 to 9000 feet"].

1876 *Helix* (*Plectopylis*) *shiroiensis*, — Hanley & Theobald, Conchologia Indica...: Plate 159, Figs 7.

1878a *Helix* (*Plectopylis*) *shiroiensis*, — Nevill, Hand list of Mollusca in the Indian Museum: 70.

1887 *Helix* (*Plectopylis*) *shiroiensis*, — Tryon, Manual of Conchology (...): 163, Plate 35, Fig. 90.

1896d *Plectopylis shiroiensis*, — Gude, Science Gossip, 3: 155–156, Fig. 20.

1899e *Plectopylis* (*Chersaecia*) *shiroiensis*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis* (*Chersaecia*) *shiroiensis*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis* (*Chersaecia*) *shiroiensis*, — Gude, The Fauna of British India (...): 105–106, Fig. 49.

Types: Naga Hills, Shiroifurar, NHMUK 1903.7.1.747 (10 syntypes).

Museum material examined: Naga Hills, Japvo Pk, 10.000 f, coll. Godwin-Austen, NHMUK 1903.7.1.748/2; Japvo Pk, Naga Hills, NHMUK 1903.7.1.3493/1; Naga Hills, Kopamedza Pk, coll. Godwin-Austen, NHMUK 1903.7.1.775/1; Burreil, Japvo Pk., coll. Godwin-Austen, NHMUK/1; Naga Hills, leg Ogle, coll. Godwin-Austen, NHMUK 1903.7.1.232/1; Shiroifurar, N.E. Manipur, Assam, coll. Godwin-Austen, NHMUK/many shells; India, Manipur, leg. Nevill, 1875, NHMUK 1891.3.17.350–351/1; India, NHMUK 1909.1.26.74(?)3;

Diagnosis: Intermediate and lower plicae present.

Description: Shell sinistral, small, spire slightly elevated, light brownish or yellowish. The 5.5–6 whorls (n=4) are separated by a deep suture (embryonic whorls are separated by shallow suture). Protoconch finely, rather regularly wrinkled with extremely fine cellular structure. The teleoconch finely reticulated; on the dorsal side of the last whorl the spiral lines are dominant, otherwise usually the radial lines; the ventral surface is also reticulated. The apertural margin is white, conspicuously thickened and strongly reflexed. The parietal callus V-shaped with the upper part of the V being shorter; there are channels at both meeting points with the lip. The prominent apertural fold continuous with the main plica. Umbilical region slightly keeled, the last half whorl is slightly angulated and dorsolaterally depressed; last half whorl situated conspicuously far from the umbilicus; with this, changing the regular infundibular shape of the umbilicus; behind the aperture, inside the last half whorl there is a slight canal.

Five specimens were opened. On the parietal wall there is a vertical lamella, which has the upper end slightly, and the lower end a bit more elongated posteriorly; main plica free from the lamella, runs until the apertural margin;

the main plica is a bit curved, with its middle portion situated close to the upper suture than the two ends; lower plica slightly shorter than the lamella; starts under the lamella; there is an additional middle plica between the main plica and the lower plica, which is approximately as long as the lamella. Palatal plicae 6, the first and second are straight, the third is slightly oblique, the fourth and fifth are almost vertical whereas the last one is extremely long and rather straight, runs along the periumbilical keel, on the side closer to the umbilicus; there is an additional free denticle posteriorly.

Differential diagnosis: See under *Chersaecia shiroiensis* subspecies 1 u. ssp.

Measurements (in mm): D= 8–8.3, H= 4.4–4.5 (n=2, NHMUK 778.03.VII.1).

Distribution: The nominotypical subspecies is known from a few localities from the Naga Hills (Figure 7.124).

Chersaecia shiroiensis subspecies 1, u. ssp.

Figures 7.2, 7.38

Material: Sikhami, Lahupa, Naga Hills, coll. Godwin-Austen, NHMUK 1903.7.1.753/7.

Diagnosis: Intermediate and lower plicae absent.

Differential diagnosis: *Chersaecia shiroiensis* subspecies 1 u. ssp. differs from the nominotypical subspecies by the fewer whorls (5.25–5.75 whorls; n=5), more prominent periostracum which results in an overall darker shell; the smoother and smaller protoconch which is conspicuously large and regularly ribbed in *Ch. shiroiensis shiroiensis*; the blunter periumbilical keel; and the absence of the intermediate and lower plicae on the parietal wall. *Chersaecia shiroiensis* subspecies 1 u. ssp. differs from *nagaensis*-like forms of *Ch. leiophis* by the smaller size, the formation of the last whorl and the absence of the lower plica.

Measurements (in mm): D= 7.6–7.8, H= 3.5–3.7 (n=3, type series).

Type locality: Sikhami, Lahupa, Naga Hills.

Distribution: The new subspecies is known from the type locality only.

Remarks: Two specimens were opened from that series type series. Observing the palatal plicae was difficult due to the corroded shells and thick shells wall. Two adult and one juvenile shells had more or less transparent shells. A very long plica was visible close to the upper "keel" in both adult shells; this long plica is situated at the place of the second plica, but the "first" plica which is usually short and situated close to the suture in other species could not be found here. The juvenile shell however, had the first, short plica visible. The other plicae of the two adult shells were short, but their morphology and orientation could not be observed without breaking the shell. In case of the juvenile shell (which was transparent), all 6 plicae are short and horizontal.

Chersaecia woodthorpei Gude 1899

Figure 7.37

1899c *Plectopylis woodthorpei* Gude, Science Gossip, 6: 15–16, Fig. 98. ["Fort Stedman, Burma"].

1899e *Plectopylis (Plectopylis) woodthorpei*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Plectopylis) woodthorpei*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Plectopylis) woodthorpei*, — Gude, The Fauna of British India (...): 124–125, Fig. 61.

1920 *Plectopylis (Chersaecia) woodthorpei*, — Gude, Journal of Molluscan Studies, 14 (2–3): 61.

Types: Burmah, Fort Stedman, leg. Woodthorpe, 1903.7.1.2100 (3 syntypes).

Museum material examined: E. Burmah, coll. Godwin-Austen, NHMUK/6;

Diagnosis: A very small, sinistral species with angulated body whorl, very slightly elevated spire, two lamellae, a main and an intermediate parietal plicae which are in contact with the anterior lamella and an overall *Plectopylis*-like palatal plication with three additional horizontal plicae anterior to the vertical plate formed by the 4th and 5th plicae.

Description: The sinistral, small, with very slightly elevated spire; whorls shouldered therefore dorsal side nearly flat; fresh shells light brown; protoconch finely tuberculated; on the dorsal side and inside the umbilicus reticulated sculpture is dominant, but on the edge of the body whorl mainly the radial lines; the 6–6.75 (n= 3) whorls are separated by moderately deep suture; peristome thickened and very much reflexed; callus also very strong, elevated, sharp, V-shaped, with the upper part of the V being shorter; the callus has two deep canals at both ends; apertural fold connected to the callus.

Two opened shells were examined. Parietal wall with a curved longer posterior and a shorter anterior lamella; both the main and the middle plicae are in contact with the anterior lamella; main plica runs until the peristome, middle plica is about half as long; lower plica slightly exceeds the posterior lamella in posterior direction, and also

runs to the peristome; palatal plicae *Plectopylis*-like, but there are three horizontal plicae anterior to the vertical plate which was formed by the accretion of the 4th and 5th plicae.

Differential diagnosis: The shell shape and the morphology of the plicae makes the identification of the species easy. A population of *Ch. perrieriae* is similar in shape, but it has only one lamella. See also under that species.

Measurements (in mm): D= 8.8–9.9, H= 3.6–4.8 (n=2, syntypes).

Distribution: *Chersaecia woodthorpei* is known from the type locality only (Figure 7.124).

Genus *Endoplon* Gude 1899a

1899a *Endoplon* Gude, Science Gossip, 6: 148.

Type species: *Helix brachyplecta* Benson 1863 by original designation.

Content: *brachyplecta* (Benson 1863) and *smithiana* (Gude 1897d).

Diagnosis: Shell dextral, flat and widely-umbilicated; protoconch almost smooth, with irregular, low growth ridges; apertural fold present; one or two vertical lamellae on the parietal wall; palatal plicae are simple, straight, the first (or the first two) and last are horizontal, the middle ones are oblique. Anatomy unknown.

Differential diagnosis: *Plectopylis* has the two lamellae connected with their upper ends, forming a lamella complex which resembles the Greek letter lambda. In one of the *Endoplon* species, however, there is a single lamella only, whereas in the other, there are two independent lamellae. Moreover, the 4th and 5th palatal plicae form a vertical plate in *Plectopylis*, whereas in *Endoplon* these plicae are more or less horizontal or oblique, not fusing to each other. See also Remarks and under *Endothyrella*.

Distribution: Myanmar (Attaram and Moulmain) (Figure 7.129).

Remarks: Both species of the genus *Endoplon* are represented in museum collection by very few empty shells. More shell material, and most importantly, ethanol-preserved samples would be necessary to decide the taxonomic position of this genus. *Endoplon* is now classified within the tribe Tribe1 due to its similar outer shell characters to *Plectopylis* species. The delimitation of *Endoplon* from *Chersaecia* is difficult without knowing the anatomy of *Endoplon* and more *Chersaecia* species. The two *Endoplon* species has the general shell shape as *Plectopylis*, but has similar plicae to *Chersaecia*. I maintain the genus on the basis of the coiling direction until more material becomes available.

Gude (1899e) classified all Vietnamese species in this genus. The revision of the Chinese species however revealed that the western (Burmese) and eastern (Chinese and Vietnamese) species are only distant relatives (see Páll-Gergely & Hunyadi 2013). For the Vietnamese former *Endoplon* species and other Chinese taxa the genus *Gudeodiscus* Páll-Gergely 2013 was erected.

Endoplon brachyplecta (Benson 1863)

Figures 7.3, 7.39

1863 *Helix brachyplecta* Benson, Annals and Magazine of Natural History, 3 (11): 319. ["ad ripas fluvii Attaran prope Moulmein"].

1868 *Helix brachyplecta*, — Pfeiffer, Monographia Heliceorum Viventium...: 396–397.

1872 *Helix (Plectopylis) brachyplecta*, — Hanley & Theobald, Conchologia Indica...: Plate 57, Figs 7, 10.

1875b *Helix (Plectopylis) brachyplecta*, Godwin-Austen, Proceedings of the Zoological Society of London, 613, Plate 74, Fig. 8.

1878a *Helix (Plectopylis) brachyplecta*, — Nevill, Hand list of Mollusca in the Indian Museum: 72.

1887 *Helix (Plectopylis) brachyplecta*, — Tryon, Manual of Conchology (...): 167, Plate 35, Figs 76, 77, 82, 83.

1897b *Plectopylis brachyplecta*, — Gude, Science Gossip, 3: 246, Fig. 37.

1899e *Plectopylis (Endoplon) brachyplecta*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Endoplon) brachyplecta*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Endoplon) brachyplecta*, — Gude, The Fauna of British India (...): 117–118, Fig. 57.

1920 *Plectopylis (Endoplon) brachyplecta*, — Gude, Journal of Molluscan Studies, 14 (2–3): 62.

Types: Ad ripas fluvii Attaran prope Moulmein, coll. Benson, NHMUK 1954.6.2.282. (syntype).

Museum material examined: Moulmein, NHMUK/1; Moulmein, Tenasserim, coll. Godwin-Austen, NHMUK 1903.7.1.749/2 (figured in Godwin-Austen 1875b).

Diagnosis: A large, dextral, robust, flat species (only apex is elevated a bit) with two lamellae, and a long main plica reaching the callus.

Description: Shell strongly built, flat, brownish, although the available specimens are mainly corroded; the 6–6.25 whorls (n=2) are separated by a deep suture. Protoconch large, matt, almost smooth and irregularly wrinkled; teleoconch finely, irregularly wrinkled and the dorsal side has some reticulated sculpture; aperture hemispheric, its upper sinus is widened, the peristome slightly reflexed and very much thickened; callus low, blunt, slightly S-shaped, with canals at both meeting points with the peristome; apertural fold connected to the callus, very long.

One opened specimen was observed. Parietal wall with two lamellae, upper end of the anterior lamella curves anteriorly, whereas the lower end slightly elongated in both the anterior and posterior directions; posterior lamella slightly reversed S-shaped. The palatal portion attached to the shell has piece broken off, and only 5 plicae were visible; all middle plicae are oblique and depressed Z-shaped or wavy; the last plica horizontal, straight.

Differential diagnosis: *E. smithiana* is larger, has shallower umbilicus, stronger callus, and most importantly, only a single lamella.

Measurements (in mm): D= 21.5–21.7, H= 7.6–7.8 (n=2, type series).

Distribution: *Endoplion brachyplecta* is known from the type locality only (Figure 7.125).

Endoplion smithiana (Gude 1897)

Figure 7.40

1897c *Plectopylis smithiana* Gude, Science Gossip, 3: 274, Fig. 38. ["Attaram, Burma"].

1897l *Plectopylis smithiana*, — Gude, The Journal of Malacology, 6: 44–45, Fig. 1.

1899e *Plectopylis* (*Endoplion*) *smithiana*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis* (*Endoplion*) *smithiana*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis* (*Endoplion*) *smithiana*, — Gude, The Fauna of British India (...): 115–116, Fig. 56.

Types: Attaram valley, leg Theobald, NHMUK 1888.12.4.1555–1556/2.

Diagnosis: A large, dextral, robust, flat species (only apex is elevated a bit) with one lamella, two short plicae anteriorly to the lamella, and a long main plica reaching the elevated callus.

Description: Shell strongly built, flat, but the protoconch is conspicuously elevated; greyish-corneous; the 5.5–5.75 whorls (n=2) are separated by a deep suture, embryonic whorls have shallow suture. Protoconch matt, irregularly wrinkled, conspicuously large (3.25–3.5 whorls, n=2); teleoconch finely, irregularly wrinkled and the dorsal side and inside the umbilicus with some reticulated sculpture; the edge of the body whorl seemingly smooth (but very finely wrinkled); aperture rounded/hemispheric, its upper sinus is widened, the peristome strongly reflexed and very much thickened; callus blunt but elevated, strongly S-shaped, with canals at both meeting points with the peristome; apertural fold connected to the callus, very long, its end is not even visible by looking in the aperture.

One opened specimen was observed. The parietal plicae was observed in the opened specimen, whereas the palatal ones in the unopened shell. Parietal wall with one curved lamella, which has both the upper and lower ends elongated posteriorly; there are two small denticles anterior to the lamella, one above, one below; under the lamella there is a short lower plica; palatal plicae 6, the first and last are straight, the second is very long and straight, the remaining ones are depressed Z-shaped and have an additional denticle above their posterior ends.

Differential diagnosis: See under *E. brachyplecta*.

Measurements (in mm): D= 27 mm (according to the original description).

Distribution: *Endoplion smithiana* is known from the type locality only (Figure 7.125).

Genus *Plectopylis* Benson 1860

1860a *Plectopylis* Benson, Annals and Magazine of Natural History, 3 (5): 244.

Type species: *Helix achatina* Pfeiffer 1845 by subsequent designation (Pilsbry 1894–1895). *Helix achatina* Pfeiffer 1845 (non *Helix achatina* Gmelin 1791: 3665) is a junior homonym, the valid name of the species is *Plectopylis bensoni* Gude 1914b.

Content: *anguina* Gould 1847, *bensoni* Gude 1914b, *cairnsi* Gude 1898, *cyclaspis* Benson 1859, *karenorum* W. Blanford 1865, *linterae* Möllendorff 1897, species 2 u. sp.

Diagnosis: Shell sinistral, flat, widely umbilicated; protoconch smooth (matt) or with small tubercles, usually with irregular, low growth ridges (wrinkles); palatal side with a vertical plate formed by the accretion of two plicae (the

4th and the 5th), and three horizontal plicae above and one below that plate; parietal wall with two vertical lamellae, they fused at their upper ends forming a structure which resembles to the Greek letter lambda (λ). Epiphallus present, penial caecum absent or very small.

Differential diagnosis: See differential diagnoses and remarks under *Chersaecia* and *Endoplion* and *Endothyrella*.

Distribution: Southern Myanmar, northern Malaysia, Myanmar and north-eastern India (Figure 7.129).

Plectopylis anguina (Gould 1847)

Figure 7.3

1847 *Helix anguina* Gould, Proceedings of the Boston Society of Natural History, 2: 218–221. [Manko, near Newville, Province of Tavoy].

1856 *Helix anguina*. — Gould, Proceedings of the Boston Society of Natural History, 6: 11.

1870 *Helix (Plectopylis) anguina*. — Hanley & Theobald, Conchologia Indica (...): Plate 13, Fig. 7.

1875b *Helix (Plectopylis) anguina*. — Godwin-Austen, Proceedings of the Zoological Society of London, 613.

1878a *Helix (Plectopylis) anguina*. — Nevill, Hand list of Mollusca in the Indian Museum: 72.

1887 *Helix (Plectopylis) anguina*. — Tryon, Manual of Conchology (...): 165, Plate 35, Figs 6.

1898e *Plectopylis anguina*. — Gude, Science Gossip, 5: 76, Fig. 79.

1899e *Plectopylis (Plectopylis) anguina*. — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Plectopylis) anguina*. — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Plectopylis) anguina*. — Gude, The Fauna of British India (...): 136–138, Fig. 69.

1964 *Plectopylis (Plectopylis) anguina*. — Johnson, The recent Mollusca of Augustus Addison Gould: 40, Plate 45, Fig. 5. (Fig. caption mixed up with *Cyclostoma [Cyclophorus] cucullata*).

Types: Tavoy, NHMUK ???/2 paralectotypes; Manko, Tavoy, coll. Gould, MCZ 147595 (paralectotype); Manko, near Newville, Tavoy, Burmah, leg. Mrs. Vinton, coll. Gould, MCZ 169042 (lectotype); Manko, near Newville, Tavoy, Burmah, leg. Mrs. Vinton, coll. Gould, MCZ 169043 (paralectotype).

Museum material examined: Burmah, Moulmein, coll. C. R. Boettger, 1908, SMF 102815; Burma, coll. Dosch ex Rolle, SMF 345109/1 (ex *Plectopylis bensoni*, SMF 172059); Mergui, NHMUK/3; Moulmein, Rangoon, Moulmein, coll. Godwin-Austen, NHMUK 1903.7.1.739/1; Rangoon, Moulmein, coll. Blanford, NHMUK 1906.1.1.732/1; Moulmein, NHMUK/1; Damathat Hill, NHMUK 1888.12.4.1553–1554/2.

Description of the type series: Shell sinistral, totally flat, the dorsal surface even concave, but the apex is elevated until the level of the body whorl, therefore it is bit elevated from the overall dorsal surface. Whorls 5–5.75 in number ($n=2$), body whorl rather bluntly keeled in the middle; whole shell brownish with yellowish stripes, but the dorsal side seems to be darker than the ventral; one of the specimens was almost completely brown above and striped below, whereas the other shells was striped above and almost completely pale ventrally; protoconch matt, almost smooth, with irregular, inconspicuous growth lines and extremely small cellular-like structure which is visible only in large magnification; teleoconch is dominated by irregular growth lines, and some reticulated areas on the dorsal surface, between the end of the protoconch and the beginning of the last whorl; edge of the body whorl almost smooth; apertural almost completely facing downwards; peristome very much thickened and slightly reflexed; callus quite low, slightly depressed V-shaped, with canals at both ends; entering fold starts in some distance from the callus.

One opened specimen was examined. On the parietal wall there is a lambda-complex with both legs having short ends elongated anterior and posteriorly, respectively; the upper branch is slightly longer than the elongation of the left leg; the main plica is connected to the right leg; palatal plicae are typical to the genus *Plectopylis*.

Differential diagnosis: *P. anguina* differs from *P. bensoni* by the lighter, flatter shell, the bluntly keeled body whorl, the more elongated aperture and the overall more elongated shells shape.

Measurements (in mm): D= 26.2–30.4, H= 7.1–7.9 ($n=2$, type NHMUK, type paralectotypes).

Distribution: The species was reported from a few South Myanmarese localities (Figure 7.126).

Remarks: Gude (1914b) mentioned that *P. anguina* differs from *P. repercuta* by some features of the parietal plication. Namely, "the lower arm of the bifurcation" is longer than the upper, whereas the reverse is true in *P. repercuta*. In one of the type specimens of *P. anguina*, which was opened, this was not the case, because the upper arm was very slightly longer than the lower. The other difference mentioned by Gude is that the lower plica does not exceed the left leg of the lambda-complex in *P. anguina*, but does in *P. repercuta*. In fact, the lower plica does not exceed the left leg in the opened paralectotype of *P. repercuta* as well. In face of the failure of confirming Gude's

observations, I keep *P. anguina* as a valid species because of its characteristic flat shell and bluntly keeled body whorl.

***Plectopylis bensoni* Gude 1898**

Figures 7.3, 7.29, 7.54, 7.93, 7.96, 7.97

Under the name *achatina*

- 1845 *Helix achatina* Pfeiffer, Zeitschrift für Malakozoologie, 2: 86. ["Südamerika"].
1850 *Helix (Atopa) achatina*, — Albers, Die Heliceen nach natürlicher Verwandtschaft systematisch geordnet: 90.
1855 *Helix (Corilla) achatinum*, — Adams & Adams, The genera of recent Mollusca; arranged according to their organization. In three volumes. Vol. II.: 208.
1859d *Helix achatina*, — Benson, Annals and Magazine of Natural History, 3 (4): 95. ["near Moulmein"]
1860a *Helix (Plectopylis) achatina*, — Benson, Annals and Magazine of Natural History, 3 (5): 244, 245.
1868 *Helix achatina*, — Pfeiffer, Monographia Heliceorum Viventium...: 395.
1871 *Plectopylis achatina*, — Stoliczka, Journal of the Asiatic Society of Bengal, 40 (2): 221, Plate 15, Figs 1–3.
1870 *Helix (Plectopylis) achatina*, — Hanley & Theobald, Conchologia Indica (...): Plate 13, Fig. 1.
1875b *Helix (Plectopylis) achatina*, Godwin-Austen, Proceedings of the Zoological Society of London, 613, Plate 74, Fig. 6.
1878a *Helix (Plectopylis) achatina*, — Nevill, Hand list of Mollusca in the Indian Museum: 71.
1879 *Helix (Plectopylis) achatina*, — Kobelt, Illustriertes Conchylienbuch 2: 236, Plate 71, Fig. 9.
1885 *Helix achatina*, — Ancey, Bulletins de la Société Malacologique de France, 2: 128.
1887 *Helix (Plectopylis) achatina*, — Tryon, Manual of Conchology (...): 165, Plate 35, Figs 3–5, 7, 8.
1889 *Helix (Plectopylis) achatina*, — Tapparone Canefri, Annali del Museo Civico di Storia Naturale di Genova, 2a (7): 47 (=323). ["Farm-Caves presso Moulmein", "Tavoy e Mergui", "Moulmein", "Nattonug", "Phathinz"]
1894 *Plectopylis achatina*, — Pilsbry, Manual of Conchology (...): 155, Plate 40, Figs 5–8.
1895 *Helix (Plectopylis) achatina*, — Godwin-Austen, Journal of the Asiatic Society of Bengal, 64 (2): 155. Plate 7, Fig. 5.
1898f *Plectopylis achatina*, — Gude, Science Gossip, 5: 114–115, Figs 80–82.
1899e *Plectopylis (Plectopylis) achatina* (and its varieties), — Gude, Science Gossip, 6: 148.

Under the name *repercuta*

- 1856 *Helix repercuta* Gould, Proceedings of the Boston Society of Natural History, 6, 11.
1868 *Helix repercuta*, — Pfeiffer, Monographia Heliceorum Viventium...: 396.
1870 *Helix (Plectopylis) repercuta*, — Hanley & Theobald, Conchologia Indica (...): Plate 13, Fig. 4.
1878a *Helix (Plectopylis) repercuta*, — Nevill, Hand list of Mollusca in the Indian Museum: 72.
1887 synonym of *Helix (Plectopylis) achatina*, — Tryon, Manual of Conchology (...): 165.
1898e *Plectopylis repercuta*, — Gude, Science Gossip, 5: 74, Fig. 78.
1914b *Plectopylis (Plectopylis) repercuta*, — Gude, The Fauna of British India (...): 146–149, Figs 78a–i.
1964 *Plectopylis (Plectopylis) repercuta*, — Johnson, The recent Mollusca of Augustus Addison Gould: 139, Plate 37, Fig. 3.

Under varieties of *achatina*

- 1898f *Plectopylis achatina* var. *obesa* Gude, Science Gossip, 5: 115, Figs 83.
1898g *Plectopylis achatina* var. *infraciata* Gude, Science Gossip, 5: 133, Fig. 84.
1898g *Plectopylis achatina* var. *venusta* Gude, Science Gossip, 5: 133, Fig. 85.
1898g *Plectopylis achatina* var. *castanea* Gude, Science Gossip, 5: 133–134, Fig. 86.
1898g *Plectopylis achatina* var. *breviplica* Gude, Science Gossip, 5: 134, Fig. 87.
1899b *Plectopylis bensoni* var. *repercutoides* Gude, Science Gossip, 5: 333.
1899e *Plectopylis (Plectopylis) repercuta*, — Gude, Science Gossip, 6: 148.
1899f *Plectopylis (Plectopylis) achatina*, — Gude, Science Gossip, 6: 175.
1899f *Plectopylis (Plectopylis) repercuta*, — Gude, Science Gossip, 6: 175.
1900a *Plectopylis achatina* var. *obesa*, — Gude, The Journal of Malacology, 7: 35–36, Fig. 13.
1900a *Plectopylis achatina* var. *infraciata*, — Gude, The Journal of Malacology, 7: 36–37, Fig. 14.
1900a *Plectopylis achatina* var. *venusta*, — Gude, The Journal of Malacology, 7: 37–38, Fig. 15.

Under the name *bensoni*

- 1914b *Plectopylis (Plectopylis) bensoni*, — Gude, The Fauna of British India (...): 138–141, Figs 70–72.
1914b *Plectopylis (Plectopylis) bensoni* var. *repercussoides*, — Gude, The Fauna of British India (...): 141–142.
1914b *Plectopylis (Plectopylis) bensoni* var. *infracasciata*, — Gude, The Fauna of British India (...): 142–143, Fig. 73.
1914b *Plectopylis (Plectopylis) bensoni* var. *castanea*, — Gude, The Fauna of British India (...): 143, Fig. 74.
1914b *Plectopylis (Plectopylis) bensoni* var. *obesa*, — Gude, The Fauna of British India (...): 143–144, Fig. 75.
1914b *Plectopylis (Plectopylis) bensoni* var. *venusta*, — Gude, The Fauna of British India (...): 144–145, Fig. 76.
1914b *Plectopylis (Plectopylis) bensoni* var. *breviplica*, — Gude, The Fauna of British India (...): 145–146, Fig. 77.
1960 *Plectopylis (Plectopylis) bensoni*, — Zilch, Handbuch der Paläozoologie...: 595., Fig. 2095.

Types: For the types of *Helix achatina*, see remarks. Other types: Tavoy and Mergui, Burmah, coll. Gould, MCZ 169336 (lectotype of *repercussa*); Tavoy, Burmah, NHMUK ??? (3 paralectotypes of *repercussa*); Moulmein, coll. Linter, NHMUK 1922.8.29.45 (holotype of *bensoni* var. *castanea*); Moulmein, coll. Linter, NHMUK 1922.8.29.43 (holotype of *bensoni* var. *infracasciata*); Moulmein, coll. Linter, NHMUK 1922.8.29.42 (holotype of *bensoni* var. *obesa*); Moulmein, coll. Linter, NHMUK 1922.8.29.46 (holotype of *bensoni* var. *repercussoides*); Moulmein, coll. Linter, NHMUK 1922.8.29.44 (holotype of *bensoni* var. *venusta*). Lectotype of *P. repercussa* was selected in Johnson (1964).

Museum material examined: Sri Lanka, leg. Tinter (probably Linter), HNHN 62599/1; Sri Lanka, Ceylon, coll. Kovács, Gy., HNHN 67067/2; Birmanie, coll. Denis, MNHN 2012-2516/1; Moulmein, Birmanie, Mission L. Fea 1885–1889, MNHN 2012-2517/7; Birmanie, coll. Jousseau, MNHN 2012-2518/2; Ceylon, ex coll. Oberwimmer, NHMSB 122190–122193/4; Indien, Moulmein, NHMSB 122182–122189/8; Indien, Moulmein, NHMSB 122180/1; Ost-Indien, ex coll. Dr. Holub 1896, NHMSK 4923/1; Mergui, leg. Fulton, coll. Möllendorff, SMF 150096/1; Burma, coll. Dosch ex Rolle, SMF 172061/2 ("var. *infracasciata*"); Barma, coll. Möllendorff, SMF 150094/1; Burma, coll. Dosch, ex Rolle, SMF 172060/2 ("*achatina obesa*"); Burma, coll. Dosch ex Rolle, SMF 172059/1 ("v. *castanea*", mixed sample with *P. anguina*); Indien, Moulmein, coll. Jaeckel ex Edlauer, SMF 212737/2; Ceylon (?), coll. Krüper ex Oberwimmer, SMF 102809/3; Ceylon, Colombo, coll. Jetschin ex Oberwimmer, SMF 102810/1; Ceylon, coll. Dosch, ex Rolle, SMF 172058/2; India, Moulmein, coll. Dosch, ex Rolle, SMF 172057/2; Ceylon, coll. Jetschin ex Oberwimmer, SMF 102812/1; Moulmein, coll. Pfeiffer ex Staudinger, SMF 102813/1; Moulmein, coll. Jetschin ex Linter 1893, SMF 102822/3; Moulmein, coll. Kobelt 1876, alte Schau-Slg. (photographed in Zilch 1960), SMF 150088/2; Birma, coll. Möllendorff ex Beddome, SMF 150091/3; Attaram-Tal, coll. Möllendorff, SMF 150092/3 (not typical form with elevated spire); Moulmein, coll. Ehrmann ex Staudinger, SMF 150093/2; Burma, coll. Reinhardt, SMF 150098/1; no locality information, SMF 150087/2; Burma, Moulmein, coll. Möllendorff, SMF 150090/3; Burma, Moulmein, coll. C. Boettger, 1908, SMF 102814/2; Burmah, Mergui, NHMUK/3 ("*anguina*"); no locality, NHMUK/2 (under the name *anguina*); Moulmein, Burmah, coll. A. S. Kennard, coll. Gude, NHMUK/2 (under the name *anguina*); Birma, coll. Dosch, ex Rolle, SMF 172063/1; Moulmein, ZMUC-GAS-1802/1; Moulmein, coll. Steenberg, ZMUC-GAS-1803/1; Indien, leg. Linter 1906, coll. Steenberg, ZMUC-GAS-1801/1; Moulmein, Bostre Indien, coll. Steenberg ex Dr. Stoliczka, ZMUC-GAS-1815/1.

New material examined: **2009.10.14-A** Myanmar, Kayin, West foot of Zwegabin Mt., Pha-an, 16°49.676'N, 97°40.504'E, 31 m, leg. Ohara, K., Okubo, K. & Otani, J. U., 14.10.2009.; **2009.10.14-B** Myanmar, Kayin, West foot of Zwegabin Mt., 16°49.552'N, 97°40.603'E, 24 m, leg. Ohara, K., Okubo, K. & Otani, J. U., 14.10.2009.;

2009.10.14-D Myanmar, Kayin, Opposite side of point C, [rubber plantation] Pha-an, 16°48.693'N, 97°39.809'E, 32 m, leg. Ohara, K., Okubo, K. & Otani, J. U., 14.10.2009.

Diagnosis: A very variable species with flat shell, rounded but shouldered body whorl, strong main plica which is connected to both the anterior lamella and the apertural fold, lower plica usually reaches the peristome.

Measurements (in mm): D= 26.2–28.8, H= 8.6–9.1 (*repercussa*, NHMUK paralectotypes); D= 23.8, H= 8.1 (holotype of *achatina* var. *castanea*); D= 17.7, H= 7 (holotype of *achatina* var. *venusta*); D= 27.3, H= 8.8 (holotype of *achatina* var. *repercussoides*); D= 21.8, H= 8.6 (holotype of *achatina* var. *infracasciata*); D= 19.3, H= 7.5 (holotype of *achatina* var. *obesa*).

Differential diagnosis: See under *P. anguina* and *P. linterae*.

Characters of the genital structure: One specimen was anatomically examined, belonging to the 20091014A sample. The left ommatophoral retractor crosses the penis and the vagina. Atrium very short; penis with longer, cylindrical proximal and shorter, also cylindrical but slightly thicker distal portion; internally penis with approx. 10 longitudinal, serrulate folds without calcareous granules; epiphallus slightly shorter than the distal, thickened part of the penis; internally with 4–5 strong, longitudinal folds; distal part of the penis and epiphallus are bound with weak

muscle fibres; a short, blunt penial caecum may be visible; the slender, flat retractor muscle is inserted on the penial caecum; vas deferens slender, even near its insertion to the pedunculus; it is bound to the proximal part of the penis and the vagina by weak membrane; vagina approximately as long as the penis; flattened at its curving point, otherwise rather cylindrical; uterus with three large, elongated embryos; diverticulum triangular, robust, short, gametolytic sac very long, slender, gametolytic sac thickened; a long, club-like spermatophore was found in the gametolytic sac; slender end of spermatophore curly; the whole surface of the spermatophore is finely wrinkled; internally spermatophore not structured.

Radula: Figure 7.97 and Table 7.4.

Distribution: The species was reported from some South Myanmar localities. Sri Lanka or Ceylon probably represents erroneous localities on the labels (Figure 7.126).

Remarks: *Helix achatina* was described by L. Pfeiffer in 1845. He erroneously wrote that the author of the taxon was Gray. The original description was based on a single specimen from the private collection of J. E. Gray, and was collected in South America. This locality was questioned later (Pfeiffer 1848: 406), and in the 5th edition of the *Monographiae Heliceorum Viventium*, Pfeiffer (1868) marked "Farm Caves, prope Moulmein" as the locality of the species. This indicates that he accepted South America as erroneous locality. The location of the single known shells is unknown. Pfeiffer's collection has been destroyed during the WWII (Dance 1986). There are two possibilities where the holotype could have ended. One is the collection of Cuming, or the shells could be remained in the collection of Gray. Both collections are deposited in the NHMUK. In face of this, I was unable to find it there. Gude (1898f) mentioned that the holotype was mentioned in Hanley and Theobald's (1870) book (locality: "Farm Caves, near Moulmein").

The only considerable difference between typical *repercussa* (type series, NHMUK) and *P. bensoni* is the very much elongated upper branch of the lambda-complex. This, however, does not allow the distinction of the two species, which otherwise does not differ in general shell shape. A sample ("Attaram-Tal", coll. Möllendorff, SMF 150092) had three shells with somewhat elevated spire, and slightly keeled body whorl (similar to that of *anguina*). This sample might be a representative of a locally isolated form with peculiar shell characters.

***Plectopylis cairnsi* Gude 1898b**

Figure 7.3

1898b *Plectopylis cairnsi* Gude, *Science Gossip* 5, 171. Figs 90 a–g. [possibly Burma].

1899e *Plectopylis (Plectopylis) cairnsi*, — Gude, *Science Gossip*, 6: 148.

1899f *Plectopylis (Plectopylis) cairnsi*, — Gude, *Science Gossip*, 6: 175.

1914b *Plectopylis (Plectopylis) cairnsi*, — Gude, *The Fauna of British India (...)*: 129–130, Fig. 64.

Type material examined: holotype NHMUK 1922.8.29.47., locality: "Burma?"

Diagnosis: A sinistral, large species with an apertural fold that is not in contact with the lambda-complex.

Description: Shell sinistral, almost flat, with the spire only slightly elevated. Whorls number 5.5. Dorsal surface a mosaic of brownish-red and paler areas. Protoconch smooth; the teleoconch very finely, regularly ribbed and decussated with fine spiral lines. The sculpture is less prominent on the ventral side of the shell. The apertural margin is thickened and slightly reflexed, with a weak parietal callus, which has two deep channels at both ends. The apertural fold usually does not reach the terminal margin of the parietal callus and is continuous with the long parietal plica.

On the parietal wall there is a lambda-like lamella-complex with an elongated upper branch and long left leg. The long plica which reaches the parietal callus is not in contact with the right leg of the lambda-complex. A short horizontal plica may be present under the lambda-complex, but free from it. On the palatal wall there are five plicae: three horizontal above and one below a vertical plica.

Measurements (in mm): D= 18.9, H= 6.5 (holotype).

Differential diagnosis: For the differences between *P. species2* u. sp., see under that species.

Distribution: Only the holotype is known without locality data.

Remarks: The species was described on the basis of a single shell.

***Plectopylis cyclaspis* Benson 1859**

Figure 7.39

- 1859a *Helix catinus* Benson, Annals and Magazine of Natural History, 3 (3): 185. ["Prope Moulmein, provinciæ Tenasserim"].
- 1859c *Helix cyclaspis* (nomen nov. pro *Helix catinus* Benson 1859a, non *Helix catinus* Pfeiffer 1856) Benson, Annals and Magazine of Natural History, 3 (3): 273.
- 1870 *Helix (Plectopylis) cyclaspis*, — Hanley & Theobald, Conchologia Indica (...): Plate 13, Fig. 10.
- 1871 *Plectopylis cyclaspis*, — Stoliczka, Journal of the Asiatic Society of Bengal, 40 (2): 222–223, Plate 15, Figs 4–6.
- 1875b *Helix (Plectopylis) cyclaspis*, Godwin-Austen, Proceedings of the Zoological Society of London, 613, Plate 74, Fig. 10.
- 1878a *Helix (Plectopylis) cyclaspis*, — Nevill, Hand list of Mollusca in the Indian Museum: 72.
- 1887 *Helix (Plectopylis) cyclaspis*, — Tryon, Manual of Conchology (...): 164–165, Plate 35, Fig. 9.
- 1897b *Plectopylis cyclaspis*, — Gude, Science Gossip, 3: 244, Fig. 34.
- 1899e *Plectopylis (Plectopylis) cyclaspis*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Plectopylis) cyclaspis*, — Gude, Science Gossip, 6: 175.
- 1914b *Plectopylis (Plectopylis) cyclaspis*, — Gude, The Fauna of British India (...): 130–132, Fig. 65.
- 1920 *Plectopylis (Plectopylis) cyclaspis*, — Gude, Journal of Molluscan Studies, 14 (2–3): 63.

Types: Benson (1859a) writes the following in the original description of *Helix catinus*: "The single specimen transmitted for examination is in such a corroded state, that the true nature of the sculpture can merely be guessed at." In the type collection of the NHMUK there are three shells with the following data: Damalthat, NHMUK 1898.12.04.1520–22/3 syntypes. These three shells surely do not represent type specimens of *P. cyclaspis*.

Museum material examined: Moulmein, Burma, coll. Oldham, Pres. 1951, NHMUK/3; Moulmein, NHMUK/2; Molmein, NHMUK/4; Burma, NHMUK 1871.9.23.48/2; Moulmain, coll. Godwin-Austen, NHMUK/2 juvenile shells; Tenasserim, Moulmein coll. Godwin-Austen, NHMUK/2 ("P.Z.S., 1874"); Moulmein, NHMUK 1906.2.2.148/4; Moulmein, Burma, coll. J. S. Hawkins, NHMUK 1954.6.2.270–271/2; Moulmein, Burmah, coll. Salisbury ex Beddome, NHMUK/3.

Diagnosis: A *Plectopylis* species with brownish purple shell and very conspicuous, sharp keel.

Description: Shell sinistral, strongly built, brownish purple, on the basal side lighter; protoconch matt, almost smooth or sometimes with extremely finely granulated and roughly wrinkled; teleoconch irregularly wrinkled, no spiral lines are visible; fresh specimens with flat periostracal folds on the keel; whorls 6.25–6.5 in number, strongly, sharply keeled, suture not conspicuous, there is an additional line (groove) which runs above the suture; umbilicus narrow; aperture strongly facing downwards; the edge of the peristome in the line of the keel is conspicuously protruding; peristome very much thickened and reflexed; callus almost straight or very slightly S-shaped; with shallow canals at both ends (the upper canal can be missing).

Two opened specimens have been examined. Left leg of the lambda-complex weak, right leg much stronger, and has a very long elongation anteriorly; upper branch also very long, parallel with the upper suture; lower plica short, does not exceed the lambda-complex; main plica missing; palatal plica typical of the genus *Plectopylis*.

Measurements (in mm): D= 18.9–19, H= 8.4–8.5 (NHMUK 148.06.2.2, n=3).

Differential diagnosis: *Plectopylis cyclaspis* cannot be mixed up with any other plectopylid species due to its conspicuous keeled whorls.

Distribution: All known samples are collected from the vicinity of Moulmein. See also Remarks and Figure 7.126.

Remarks: *Plectopylis revoluta* (Pfeiffer 1867) is probably the synonym of *P. cyclaspis* (see Gude 1914b). Stoliczka (1871) claims that the type locality of *P. revoluta* (Andaman Islands) is probably incorrect, because he received thousands of other shells from those islands, but none of them were plectopylids.

***Plectopylis karenorum* W. Blanford 1865**

- 1865 *Helix (Plectopylis) karenorum* Blanford, Journal of the Asiatic Society of Bengal, 34 (2): 73–75, 94. ["Banks of Tsanda Khyoung, near Kaintha village, in Henzada district, Pegu" "on the banks of the Nungatho Khyoung, Henzada district"]
- 1868 *Helix karenorum*, — Pfeiffer, Monographia Heliceorum Viventium...: 397.
- 1869 *Helix karenorum*, — Pfeiffer, Novitates conchologicae. Series prima...: 503, Plate 108, Figs 16–18.
- 1870 *Helix (Plectopylis) karenorum*, — Hanley & Theobald, Conchologia Indica (...): Plate 13, Fig. 6.
- 1875b *Helix (Plectopylis) karenorum*, — Godwin-Austen, Proceedings of the Zoological Society of London, 613, Plate 74, Fig. 5.

- 1878a *Helix (Plectopylis) karenorum*, — Nevill, Hand list of Mollusca in the Indian Museum: 72.
 1887 *Helix (Plectopylis) karenorum*, — Tryon, Manual of Conchology (...): 164, Plate 35, Figs 96–100.
 1897b *Plectopylis karenorum*, — Gude, Science Gossip, 3: 244–245, Fig. 35.
 1899e *Plectopylis (Plectopylis) karenorum*, — Gude, Science Gossip, 6: 148.
 1899f *Plectopylis (Plectopylis) karenorum*, — Gude, Science Gossip, 6: 175.
 1914b *Plectopylis (Plectopylis) karenorum*, — Gude, The Fauna of British India (...): 132–134, Fig. 66.

Types: No specimens of *P. karenorum* were found in the type collection of the NHM. The samples collected by Blanford and labelled as being collected from one of the type localities are probably syntypes.

Museum material examined: Pegu, coll. Möllendorff, SMF 150097/1; Pegu, Henzadah, coll. Blanford, NHMUK 1906.2.2.146/5; Herizadah, NHMUK/7; Pegu, Burmah, coll. A. S. Kennard, NHMUK/1; Moulmain?, coll. Godwin-Austen, NHMUK 1903.7.1.735/1; Pegu, Burma, NHMUK/3; Burmah, coll. Godwin-Austen, NHMUK 1903.7.1.737/3; Henzada District, NHMUK 1888.12.04.1548–1550/3; Pegu, excoll H. Adams, NHMUK 1878.1.28.283/1; Pegu, Nungathokhyoung, Henzadah, coll. Blanford, NHMUK 1906.2.2.263/2;

Diagnosis: A small, fragile species of *Plectopylis* having lighter and darker striped resulting in a mosaic structure. The angled body whorl and therefore, entirely flat dorsal surface is characteristic for the species.

Description: Shell sinistral, relatively small and fragile, completely flat; colour basically greyish with brownish-corneous stripes; protoconch extremely finely tuberculated and roughly, irregularly wrinkled; whorls 5.5–6, separated by relatively shallow suture; whorls angled, their upper side flat; whole shell with fine reticulated sculpture; on the dorsal side and inside the umbilicus the spiral lines are stronger than the radial, or the two type of lines are of equal strength, but the side of the body whorls is dominated by radial wrinkles; aperture solid, rather rounded, peristome slightly thickened and reflexed; callus well-developed but blunt, slightly S-shaped, the upper part of the S is shorter; there are two deep canals at both ends; of the callus; apertural fold in contact with the callus.

Three opened specimens were examined. Left leg of the lambda-complex with a posteriorly elongated lower end; upper branch is also well-developed, approximately as long as the posteriorly elongated part of the left leg; right leg with anteriorly and somewhat obliquely elongated lower end; main plica in contact with the right leg; palatal plicae is typical to that of *Plectopylis*.

Measurements (in mm): D= 12–14.1, H= 3.9–5.1 (n=4, NHMUK 1906.2.2.146); D= 18.4–19.7, H= 5.6–5.9 (n=2, NHMUK 1906.2.2.263).

Differential diagnosis: *Plectopylis karenorum* can be distinguished by all congeners by the flat, solid, thin-walled shell with shouldered body whorl and striped coloration. *P. goniobathmos* has more elevated spire and rounded whorls and its two lamellae are independent from each other. *P. feddeni* also have the two lamellae separated.

Moreover, the main plica of *P. feddeni* is independent from the callus, whereas they are in contact in *P. karenorum*.

Distribution: This species has been reported from a few Burmese localities (Figure 7.126).

Plectopylis linterae Möllendorff 1897

Figures 7.3, 7.29

1897 *Plectopylis linterae* Möllendorff, Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 29, 28–29. ["Pegu"].

1898h *Plectopylis linterae*, — Gude, Science Gossip, 5: 170, Fig. 88.

1898h *Plectopylis linterae* var. *fusca* Gude, Science Gossip, 5: 170–171, Fig. 89.

1899e *Plectopylis (Plectopylis) linterae* and *linterae* var. *fusca*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Plectopylis) linterae* and *linterae* var. *fusca*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Plectopylis) linterae*, — Gude, The Fauna of British India (...): 134–136, Fig. 67.

1914b *Plectopylis (Plectopylis) linterae* var. *fusca*, — Gude, The Fauna of British India (...): 136, Fig. 68.

Types examined: Pegu, coll. Möllendorff, SMF 9280 (lectotype);

Museum material examined: Pegu, coll. Dosch, ex Rolle, SMF 172062/2; Pathung-Thoung, Attaram R., NHMUK 1888.12.4.1541–1543/3; Burma, NHMUK 1916.3.16.5/1;

Diagnosis: A strongly built species with slightly elevated spire, very much thickened peristome, and a main plica which is quite weak, sometimes do not reach the apertural fold.

Description: Shell sinistral, strongly-built, relatively small, spire somewhat elevated, dorsal surface slightly conical; shell outline slightly oval; colour dark yellowish-greyish to brownish; protoconch matt, very finely, irregularly wrinkled with extremely fine cellular structure; whole shell is dominated by irregular, fine wrinkles, but on the dorsal

side and inside the umbilicus spiral lines can make the sculpture reticulated; periumbilical area smooth; whorls 5.25–5.75 (n=3), rounded, umbilicus infundibular; there is a blunt keel around the umbilicus; peristome very much thickened and slightly reflexed; callus elevated, strong, S-shaped with canals at both ends; apertural fold strong, in contact with the callus.

One opened shell was examined. both legs with slightly elongated ends anterior and posteriorly as well; upper branch as long as the extension of the left leg; main plica attached to the right leg, but does not reach the apertural fold (in other specimens however, does, but the main plica is always much weaker than the apertural fold); main plica in contact with the right leg; palatal plicae is typical to that of *Plectopylis*.

Measurements (in mm): D= 15.7–16.2, H= 5.6–6.6 (n=3, lectotype and paralectotypes); D= 16–16.9, H= 5.4–5.5 (n=3, var. *fusca*, NHMUK 88.12.4.1541–43).

Differential diagnosis: Typical *P. linterae* specimens are much smaller than *P. bensoni*, have more elevated spire and have more rounded body whorl. Although in some (probably very old) specimens of *P. linterae* the apertural fold is connected to the main plica, the apertural fold is always much stronger (more elevated) than the main plica. These two plicae are always connected in *P. bensoni*, and their boundary is not visible.

Distribution: *Plectopylis linterae* is known from Pegu only. The exact geographic position of the other locality (Pathung-Thoung) is unknown (Figure 7.126).

Plectopylis species2 u. sp.

Figures 7.3, 7.29, 7.32, 7.39, 7.55, 7.93, 7.96, 7.97

1960 *Plectopylis revoluta*, van Jutting, Basteria, 24, 17. ["Limestone hill Kaki Bukit near kampong Wang Tangga, Perlis"].

1963 *Plectopylis revoluta*, Berry, Malayan Nature Journal, 17, 13. ["abundant in limestone hills in North Malaya"].

2001 *Plectopylis revoluta*, Maassen, De Kreukel, Extra Editie: page number unknown.

Type material: Malaysia, Perlis, Kaki Bukit (N of Kangar), leg. Hemmen, J. & Ch., October 1998, HNHM 97469 holotype, JH/11, PGB/9, NHMW 108117/2; Malaysia, Perlis, Bukit Kubu (NE of Kuala Perlis), leg. Hemmen, J. & Ch., 21.03.1998., JH/5, PGB/4; Malaysia, Perlis, Wangga Tangga Valley near Kaki Bukit, leg. Hemmen, J. & Ch., 23.03.1998., HA/1, JH/10, PGB/9; Malaysia, Naha-Krabi, south, leg. Dieter Hörner, April 2003., GJ/3; Malaysia, Perlis, about 21 km N of Kangar, max. 3 km from the Thai border, Kaki Bukit near Kampung Wang Tangga, 6°38'28"N, 100°12'08"E, in leaf litter in a secondary forest, on a base of a limestone hill, leg. Kessner, V., 17.03.1995., PGB/1, REI/3 paratypes and one juveniles shell (not paratype); Gua Kelam towards Wang Tangga, near fossil locality site, Kaki Bukit, Titi Tinggi Mukim, Perlis, West Malaysia, live/dead collected among disturbed limestone rocks and litters near exit of cave, leg. Chan Sow-Yan & Leo Nguang, 26.4.1996, ex Chan 1997, SMF 311305/2; leaf litter in karst area, Perlis, Malaysia, DC RG391.2/2 specimens; West Malaysia, Perlis, Kaki Bukit, Gua Kelam, 06°38.68'N 100°12.23'E, leg. Maassen, W., 09.07.1999. WM/35; West Malaysia, Perlis, Wang Kelian State Park near Thai Border, 06°41.98'N 100°11.80'E, leg. Maassen, W., 10.07.1999., WM/44; West Malaysia, Perlis, limestone hill, 30 km N of Kangar, 06°41.00'N 100°11.21'E, leg. Maassen, W., 10.07.1999., WM/10; West Malaysia, Perlis, Bukit Air Park, N of Kangar, leg. Maassen, W., 11.07.1999., WM/5; West Malaysia, Perlis, Kaki Bukit, near Kampung Wang Tangga, leg. Kessner, V., 11.07.1995., WM/4; Thailand, Prov. Satun, Ban Rae. Coll. Brandt, 1966, MNHN/3; Thailand, Satun: Ban Rae, leg. Brandt, 04.01.1966. ZMH 45914/4; same data, SMF 207667/3; same data, Coll. Klemm, (Nr. 54168), NHMW 108223/2; same data, Coll. Oberwimmer, NHMW 108224/3; same data, coll. Biggs, NHMUK ???/4; same data, coll. Brand 1966, MNHN 2012-2519/3; Kaki Bukit, near Kampung Wang Tangga, Perlis, Malaysia, in leaf litter, secondary forest at the base of limestone hill, leg. Kessner, V., 17.03.1995., HNHM42264/1; Malaysia, Perlis, Kaki Bukit, Kampunk, Wang Tangga, coll. Drimmer, L., MMGY 69644/2.

Diagnosis: A sinistral, medium-sized, brown-shelled species having periostracal filaments along the upper keel of the body whorl in living specimens. The apertural fold is not in contact with the terminal margin of the parietal callus. The lambda-like parietal lamella-complex has a short plica on the anterior side. This plica is fused to the anterior foot of the lambda-complex.

Description: The chocolate brown (or yellowish, if weathered) shell is sinistral and flat with slightly raised apex. The 6–6.5 whorls are separated by a relatively shallow suture. The protoconch is large, almost smooth on the first two whorls, and has inconspicuous growth lines on the later whorls. The ventral surface of the protoconch (as viewed from the dorsal, umbilical side) is roughly ribbed. The teleoconch has a reticulated surface with very fine, dense ribs and widely-spaced spiral lines. In fresh specimens the periostracum has deciduous folds on the upper keel of the

body whorl. The apertural margin is thickened and slightly expanded. There is a sharp parietal callus, which has channels at both ends at the meeting point with the lip. The apertural fold is usually short, white and never in contact with the terminal margin of the parietal callus.

Four specimens were opened. On the parietal wall there is a lamella-complex with a relatively short left leg and short upper branch. There is also a short horizontal plica attached to the middle of the right leg, and this is rarely in contact with the long horizontal plica. A short horizontal plica is also present below the lambda-complex. In some specimens the horizontal plica that is anterior to the lambda-like lamella-complex is connected to the apertural fold. On the palatal wall there are six plicae, the first three are straight with sinuate (S-shaped) posterior ends. The last plica is slightly curved with its convex side pointing upwards. An additional short plica is visible above the posterior end of the last plica. The fourth and fifth plicae are vertical and fused together, forming a single straight plica. This straight plica is usually bifurcated below and has 1–2 additional horizontal plica attached to it posteriorly.

Measurements (in mm): D= 17.6–19.0, H= 6.6–7.2 (n=4).

Differential diagnosis: *Plectopylis* species2 u. sp. differs from *P. cairnsi* by its darker shell, thinner lip, less rounded body whorl, several additional plicae on the palatal wall, and shorter left leg and upper branch of the lambda-complex. The lambda-complex of *P. cairnsi* is never fused to the long horizontal anterior plica, and *P. species2* u. sp. has a small fold attached to the central part of the right leg. *Plectopylis bensoni* is usually larger and has a rounded body whorl, whereas *P. species2* u. sp. has the body whorl obliquely depressed from lower lateral direction. Moreover, *P. species2* u. sp. has finely reticulated shell surface, which is smooth in *P. bensoni* with irregular growth lines.

Radula: Figure 7.97 and Table 7.4.

Type locality: Malaysia, Perlis, Kaki Bukit (N of Kangar).

Distribution: *Plectopylis* species2 u. sp. is known only from Perlis Province (near the Thai Border) in Northern Malaysia and Satun Province in Southern Thailand (Figure 7.126). See also Remarks.

Remarks: The species collected from Northern Malaysia was referred to as *Plectopylis revoluta* (Pfeiffer 1867) in the literature (see above). *P. revoluta* however, was originally described from the Andaman Islands. Gude (1914b) discussed the taxonomic status of *P. revoluta* in detail, and concluded that *revoluta* is possibly a synonym of *Plectopylis cyclaspis*.

The sample collected by Brandt in 1966 was distributed in several museums (ZMH, NHMW, SMF, MNHN). According to the label the locality is "Satun: Ban Rae". The locality name "Ban Rae" probably refers to Ban Rae Kot, northwest from Mueang Satun.

Tribe2 new tribus

Type genus: *Sinicola* Gude 1899.

Content: Genus2 u. gen., *Gudeodiscus* Páll-Gergely 2013, *Halongella* Páll-Gergely 2015, Genus3 u. gen., *Sicradiscus* Páll-Gergely 2013, *Sinicola* Gude 1899e.

Diagnosis: Shell sinistral (most *Endothyrella*) or dextral (one *Endothyrella* species and species of all other genera). The majority of species possess a somewhat elevated spire; protoconch usually regularly, finely ribbed; parietal lamellation relatively simple usually without long main and lower plicae. Penial caecum present in most species.

Differential diagnosis: See under Tribe1.

Genus2, u. gen.

Type species: Genus2 species3 u. sp.

Content: *andersoni* (Blanford 1869), species3 u. sp.

Diagnosis: Shell dextral, body whorl keeled (angulated); protoconch with reticulated sculpture (both spiral lines and fine regular ribs); palatal plicae slightly sinuate; a single lamella sometimes with additional horizontal plicae on the parietal wall. Anatomy unknown.

Differential diagnosis: Genus2 gen. nov. differs from *Sinicola* by the presence of spiral sculpture on the protoconch. The protoconch of Genus3 gen. nov., has only radial sculpture, and the shells have rounded body whorls.

Distribution: Middle Laos. One species (*P. andersoni*) lives on the Myanmar-Chinese border region (Figure 7.129).

Genus2 *andersoni* (W. Blanford 1869)

Figures 7.4, 7.32

- 1869 *Helix (Plectopylis) andersoni* Blanford, Proceedings of the Zoological Society of London: 448 [Bhamo in regno Avæ et Hoetone in Yunan].
- 1874 *Helix andersoni*, — Hanley & Theobald, Conchologia Indica... : 46, pl. 112, Figs 8–9 [Bhamo, and Hoetone in Yunan] (1870–1876).
- 1875 *Helix (Plectopylis) andersoni*, — Godwin-Austen, Proceedings of the Zoological Society of London: 612, pl. 74, Fig. 9.
- 1885a *Plectopylis Andersoni*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 12: 389 ["bei Bhamo in Oberbirma", "»Hoitone« in der chinesischen Provinz Yünnan"].
- 1886 *Plectopylis Andersoni*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 188.
- 1887 *Helix andersoni*, — Tryon, Manual of Conchology. 2 (3): 161, pl. 34, Fig. 71; pl. 35, Figs 74–75 [Bhamo, in Ava; Hoetone, In Yunan].
- 1889 *Helix (Plectopylis) Andersoni*, — Tapparone Canefri, Annali del Museo Civico di Storia Naturale di Genova, 2a (7): 47 (=323). ["Catcin di Pun-Can, Cimfò, Monti Est di Bhamó", "Bhamó, Hoetone"]
- 1896c *Plectopylis andersoni*, — Gude, Science Gossip, 3: 154, Figs 17a–c [Near Bhamo and Ava, in Upper Burma and on the Yunnan-frontier].
- 1899e *Plectopylis (Chersaecia) andersoni*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Chersaecia) andersoni*, — Gude, Science Gossip, 6: 175.
- 1914b *Plectopylis (Chersaecia) andersoni*, — Gude, The Fauna of British India including Ceylon and Burma. Mollusca II. (Trochomorphidae – Janellidae), 2: 73, 114, Figs 55a–c.

Types: According to Dance (1986) the collection of Blanford is deposited in the British Museum (now: Natural History Museum, London). In the type collection of the NHMUK I have not found syntypes, but there is a sample (NHMUK 1906.02.02.364) which is labelled as being collected from Bhamo, one of the type localities. This sample may represent the type lot.

Museum material examined: Yünan, Slg. Bosch, ex H. Rolle (1 juv.), SMF 172066; alte Schau-Slg/2, SMF 150117; no locality information (alte Schau-Slg.), SMF 150117/2; Upper Indwadi, NHMUK 1888.12.04.1561/2; Burma, coll. A. S. Kennard, ex Gode, NHMUK/2; Bhamo, Upper Burma, NHMUK 1906.02.02.364/5; Khakhyan Hills, Burmah, coll. Godwin-Austen, NHMUK/3; Bhamo, NHMUK/1.

Diagnosis: A very large, lenticular, angulated species with elevated, sharp callus.

Description: Shell flat, angulated, light brown or corneous; ventral side of the body whorl keeled around the moderately wide, very deep umbilicus; protoconch with very fine ribbed structure and spiral striae of the same strength; teleoconch equally ornamented with fine ribbing and spiral striae, resulting in rough, irregular reticulated surface; 7.5–8.5 slowly increasing whorls separated by shallow suture; near the sutures the riblets sometimes supported with fine folds of the periostracum; aperture rounded, with white, slightly expanded and thickened apertural rim; callus slightly elevated, sharp, slightly S-shaped and forms two canals upon junction with the lip.

Parietal wall with one curved horizontal lamella; palatal side with eight horizontal plicae, first near the suture, the second is very small; the last also short and close to the lower suture and the penultimate resembles the second denticle; remaining four plicae between the first and last two are long and slim.

Measurements (in mm): D= 24.6–27.2, H= 10.9–11.4 (n=2, RBINS I. G. 10591, Burmah).

Differential diagnosis: This species differs from large Chinese *Gudeodiscus* species (and Genus3 *laomontana*) by the keeled margin of the shells. It is much larger than all *Sinicola* species. The largest *Sinicola* species, *S. fimbriosa* does not have a callus and has a stronger apertural margin.

Distribution: The species is known from Northern Burma and Western Yunnan. Hoetone (Hutung Village) and Bhamo are located in Kachin Provinces, whereas Ava is in Mandalay Province (all in Burma/Myanmar). The Kakhyen Hills are situated on the Chinese (Yunnan) and Burmese (Kachin) border (Figure 7.125).

Remarks: I found only one old museum sample, which was collected in China (SMF 172066). The description of the lamellae and plicae is based on Gude (1896c). I had no possibility to observe the armature.

Genus2 species3 u. sp.

Figures 7.4, 7.29

1953 *Plectopylis laomontana*, Saurin, *Journal de Conchyliologie*, 93 (4), 113.

Type material (juvenile shells are not types): Laos, Pa Hia (Ancienne province Tran Ninh), Coll. Saurin, MNHN 24947 holotype, MNHN 24948/6 paratypes + 6 juvenile shells, HNHM 97470/2 paratypes; Laos, Pah Xieng Tong,

Pa Hia, Prov. Tran Ninh, Coll. Saurin, MNHN 249479/1 paratype + 1 juvenile shell; Laos, Pa Ka Tai, Prov. Tran Ninh, Coll. Saurin, MNHN 24950/5, HNHN 97471/1; Laos, Pa Xieng Tong, Pa Hia, Prov. Tran Ninh, Coll. Saurin MNHN 24951/3; Laos, Pa Hia (Tran Ninh), Coll. Saurin, MNHN 24952/1 juvenile shell.

Diagnosis: A dextral, medium-sized or large species with a relatively sharp upper keel and a blunt lower keel on the body whorl. On the parietal wall there is a single oblique lamella with a horizontal plica below it.

Description: The shell is yellowish or corneous (the type material consists mainly of weathered shells). The protoconch is very large, with regular riblets and spiral lines; the ribs are more prominent than the spiral sculpture. The 5.25–6 whorls are separated by a shallow suture. The umbilicus is wide but moderately deep. The body whorl has a prominent upper keel and a less conspicuous lower keel. The apertural margin is slightly thickened. The parietal callus is not well developed and is only clearly apparent in older specimens.

Three shells were opened. On the parietal wall there is a single curved lamella that is oblique, its upper end situated much more anteriorly than the lower end. A short, but thick vertical plica is situated below and anteriorly of the lamella. On the palatal wall there are six more-or-less parallel plicae, with some additional short plicae. The most prominent additional plica is situated above the posterior end of the last plica. The fifth plica is usually S-shaped.

Measurements (in mm): D= 16.3–21.3, H= 6.7–8.6. (n=4, shells from different samples)

Differential diagnosis: Genus 2 species 3 u. sp. is smaller than *P. andersoni*, its keel is situated higher (this results a more angular body whorl), has weaker parietal callus, a lower horizontal plica on the parietal wall which is absent in *andersoni*.

Type locality: Laos, Pa Hia (Ancienne province Tran Ninh).

Distribution: This species is known only from Southern Laos (Figure 7.125).

Remarks: The exact localities from which this species was collected are unknown (See Saurin 1953).

Genus *Endothyrella* Zilch 1960

1899e *Endothyra* Gude (section of *Plectopylis*): Science Gossip, 6: 148., non *Endothyra* Phillips 1845 (Foraminifera).

1960 *Plectopylis* (*Endothyrella*) Zilch: Handbuch der Paleozoologie, 6 (2).

1999 *Endothyrella*, Schileyko: Treatise on Recent Terrestrial Pulmonate Molluscs, Part 4(...): 2: 460.

Type species: *Helix plectostoma* Benson 1836, by original designation.

Content: *aborensis* (Gude 1915), *affinis* (Gude 1896), *babbagei* (Gude 1915), *bedfordi* (Gude 1915), *blanda* (Gude 1897), *brahma* (Godwin-Austen 1879a), *fultoni* (Godwin-Austen 1892), *gregorsoni* (Gude 1915), *hanleyi* (Godwin-Austen 1879b), *macromphalus* (W. Blanford 1870), *minor* (Godwin-Austen 1879b), *miriensis* (Gude 1915), *munipurensis* (Godwin-Austen 1875b), *oakesi* (Gude 1915), *oglei* (Godwin-Austen 1879a), *pinacis* (Benson 1859) (syn: *pettos* von Martens 1868), *serica* (Godwin-Austen 1875b), *sowerbyi* (Gude 1898), *williamsoni* (Gude 1915).

Diagnosis: Shell sinistral or dextral; protoconch usually finely, regularly ribbed (see remarks on the protoconch of dextral species); umbilicus usually relatively narrow; apertural fold absent; horizontal main plica usually absent; low parietal plica runs close to and parallel with the lower suture, it is usually very short, but in some species it reaches the callus; usually periostracal folds on the shell are standing in 3–7 lines; folds hair-like in most species, resulted by the rolling of flat folds; folds flat (not rolled and slender) in some species; dorsal sculpture strong, usually reticulated; usually one (sometimes two) vertical parietal lamella with denticles posteriorly (probably the remains of the posterior lamella); palatal plicae complicated in most species with many small denticles; in many species they are divided in the middle.

Penis internally with hollows having calcareous granules inside; epiphallus may be longer than penis and enters penis laterally; small penial caecum present; diverticulum (if present) and gametolytic sac are of the same size.

Differential diagnosis: All known species of the genera *Sinicola*, *Gudeodiscus* and *Sicradiscus* are dextral.

Regardless of the coiling direction, most *Endothyrella* species differs from *Sinicola* by the presence of usually hair-like periostracal folds standing in multiple lines. Deciduous folds in *Sinicola* are present only along the keel and the folds are always flat. Most *Sinicola* species (especially the large species) have sharp keel, whereas *Endothyrella* species have usually rounded or slightly keeled, shouldered body whorl. The palatal plicae of *Sinicola* are usually simple, horizontal, straight and parallel, but in *Endothyrella* they are more complex, namely often oblique or even vertical, divided and ornamented with minute denticles posteriorly. In *Sinicola* the posterior lamella is present on the parietal wall, with two horizontal plicae anteriorly above and below, whereas in most *Endothyrella* species (except for *E. aborensis*) the anterior lamella is present and the posterior is missing or dissolved into two short vertical plicae.

Gudeodiscus species never have deciduous folds of the periostracum, and sometimes they have fold in the aperture. The very tiny, pointed periostracal folds of *G. phlyarius* (Mabille 1887) standing in multiple lines on the body whorl (see Páll-Gergely & Hunyadi 2013, Fig. 113) are not homologous with the long hair-like folds of *Endothyrella*. Palatal plicae in *Gudeodiscus* are usually depressed Z- or L-shaped and posterior small denticles are very rare (except for one denticle above the posterior end of the last plica), whereas the palatal plicae of *Endothyrella* are frequently divided in the middle and posterior small denticles are usual. In *Endothyrella* the anterior lamella is present, and often the upper horizontal plica is missing whereas in *Gudeodiscus* both lamellae or only the posterior one is visible and the upper horizontal plica (above the lamella) is almost always present. Additionally, *Gudeodiscus* species have exactly rounded body whorl, but in many *Endothyrella* species the body whorl is rather "flattened" from lateral direction.

The genus *Sicradiscus* seems to be the closest relative of *Endothyrella* because of the weak or sometimes reduced posterior lamella. Moreover, juvenile specimens of *Sicradiscus transitus* Páll-Gergely 2013 have hairs standing in two spiral lines on the body whorl. The homology of the hairs standing in spiral lines in *S. transitus* and in *Endothyrella* is, however, questionable. In *Endothyrella* the hairs are arranged in 3–7 spiral lines, whereas in *S. transitus* they are standing only in two rows. This trait seems to be absent in adult *S. transitus* shells and all other species of *Sicradiscus*, but common in fully grown *Endothyrella* shells. The two genera (i.e. *Endothyrella* and *Sicradiscus*) differ in the short, straight palatal plicae which are usually connected in *Sicradiscus* and longer, more complex palatal plica sometimes having additional denticles in *Endothyrella*. In both genera divided plica may occur, but in case of *Sicradiscus* the posterior fourth and fifth plica seems to be always connected, whereas in *Endothyrella* all plicae are free. Moreover, western *Sicradiscus* species (*feheri* Páll-Gergely 2013, *invius* (Heude 1885), *mansuyi* (Gude 1908b), *securus* (Heude 1885) and *transitus*) differ from *Endothyrella* by the presence of a strong apertural fold.

Plectopylis, *Endoplion* and some *Chersaecia* species have granulated or smooth protoconch, whereas it is finely ribbed in *Endothyrella*. Moreover, these three genera usually have a long apertural fold which sometimes connects the anterior lamella with the aperture. See also under *Chersaecia*.

Distribution: The distribution of the genus is restricted to Nepal and northeastern India and one species (*E. plectostoma*) was reported from Myanmar (Figure 7.128).

***Endothyrella aborensis* (Gude 1915)**

Figures 7.28, 7.41

1915 *Plectopylis* (*Endoplion*) *aborensis* Gude: Records of the Indian Museum, 8: 511–512, plate 42, Figs 3a–d.

["Between Renging and Rotung, 2200 ft., Abor country."]

2013 *Endothyrella aborensis*, — Páll-Gergely & Hunyadi: Archiv für Molluskenkunde, 142 (1): 5.

Types: According to the original description, two shells, an adult and a juvenile were collected and finally deposited in the Indian Museum (inventory numbers: 5998 and 6135). The material from the Indian Museum is moved to the ZSI. I contact them, and received two low-quality photos of an adult *Endothyrella* shell, which clearly showed a different specimen than the one figured in Gude (1915).

Diagnosis: A small (14 mm), sinistral, almost flat, widely umbilicated species with strong callus, Z or L-shaped palatal plicae, two parietal lamellae, a short upper plica which is in contact with the posterior lamella, and a long lower plica which reaches the peristome.

Differential diagnosis: The species was not examined by us, but according to the original description the species differs from all congeners by the short and uniquely shaped palatal plicae, which are depressed Z-shaped, or the lower branch of the "Z" is elongated.

Remarks: So far, this is the only *Endothyrella* species with two well-developed lamellae. The parietal lamellae show a very unusual arrangement which has not been observed in any other species of Plectopylidae. The two parietal plicae can be the result of teratological duplication which has already been published in case of several species (see under the "evolution of the parietal plicae and lamellae").

Distribution: The species is known from the type locality only (approximately 28°10'N, 95°13'E) (Figure 7.122).

***Endothyrella affinis* (Gude 1897)**

Figures 7.24, 7.41

1897c *Plectopylis affinis* Gude: Science Gossip, 3: 276, Figs 41a–d. ["Khasia Hills, Assam"].

1897l *Plectopylis plectostoma* var. *tricarinata*, — Gude, The Journal of Malacology, 6: 46–48, Fig. 3.
1899e *Plectopylis (Endothyra) affinis*, — Gude: Science Gossip, 6: 148.
1899f *Plectopylis (Endothyra) affinis*, — Gude: Science Gossip, 6: 175, 176.
1914b *Plectopylis (Endothyra) affinis*, — Gude: The Fauna of British India...: 73, 84–85, Figs 34a–d. ["Assam : Khasi Hills"].

Types: Khasia Hills, NHMUK 1901.4.25.41–43/3 (paratypes?); India, Khasia Hills, ex Fulton, NHMUK 1922.8.29.26 (holotype); N-Vorderindien, Khasi-Berge, coll. C. R. Boettger 1911, SMF 118096/1 paratype; Cherrapoonjee, coll. Jetschin ex coll. Gude 1900, SMF 118095/2.

Material examined: India, Khasi Hills, NHMW 34233/2; Khasi Hills, coll. Möllendorff, SMF 150107/3; Naraindher, Cachar, Ede, coll. Godwin-Austen, NHMUK 1903.7.1.1666/15 (several of them are juveniles); Khasi-Berge, coll. Möllendorff, ex coll. Gude, SMF 9279/4; Khasi Hills, coll. Dosch ex coll. Rolle, SMF 172074/2; India, "showing immature armature", NHMUK 1916.3.15.1.2/2; Khasi Hills, Assam, coll. Salisbury ex coll. Beddome, NHMUK/3; Khasi Hills, NHMUK/3; India, Khasi Hills, NHMUK 92.9.22.1–4/4; Khasi Hills, figured in Godwin-Austen (1874), NHMUK 1903.7.1.759/11; Khasi Hills, coll. Jetschin, ex coll. Linter 1893, SMF 118087/1; N. O(?) Indien, coll. Steenberg, ZMUC-GAS-1811.

Diagnosis: A small (ca. 10 mm), sinistral, yellowish species with narrow umbilicus, conical dorsal surface and slightly shouldered body whorl. Hairs are arranged in four rows on the body whorl. Callus strong, middle palatal plicae usually divided in the middle; the posterior fragments are oblique, the anterior ones are rather straight; parietal wall with a single, slightly curved lamella with short denticles posteriorly, one above and one below, and a horizontal lower plica which may be divided in the middle.

Differential diagnosis: *E. affinis* resembles to *E. plectostoma*, which is somewhat smaller, darker, has a horizontal, relatively long plica anterior to the lamella (probably not homologous with the upper plica), and has the periostracal folds arranged on five spiral line, whereas in *E. affinis* there are four hair rows. Moreover, the umbilicus of *E. plectostoma* is narrower and its spire is more elevated.

Distribution: The species is recorded from the type locality only (Figure 7.123).

Endothyrella species4 u. sp.

Figures 7.26, 7.40

Material: PL001 Nepal, Taubas, Bhainse, Makwanpur District., 27°49'25.21"N, 85°04'48.39"E., leg. Budha, P., 30.03.2012.. Holotype (CDZMTU018); paratypes from the type locality (CDZMTU019, 5 Juv. shells, not paratypes).

Diagnosis: A small species with flat dorsal part and conspicuously shouldered (keeled) body whorl. Hairs are arranged in four rows. Parietal lamella simple with a short free horizontal plica below it, and two denticles posterior to the lamella which are in contact with the it; middle palatal plicae divided.

Description: Shell sinistral, semi-transparent, with flat apical part; protoconch elevates from the dorsal surface; colour brownish or greyish; protoconch conspicuously large, consists of 2.5, 2.75 whorls, very finely, regularly ribbed; teleoconch with well-visible reticulated sculpture dominated by radial growth lines; sculpture somewhat weaker on the ventral surface; very slender, long periostracal folds (hairs) standing in four spiral lines along the body whorl (two closely adjacent and running with the keel above, one around the umbilicus depression and one intermediate), whorls 6.25 (Holotype) moderately bulging, separated by relatively deep suture; umbilicus wide and deep; apertural lip thin, slightly reflexed; callus moderate; no fold in the aperture.

One specimen was opened. Palatal wall with a single, straight lamella, with two short denticles on the posterior side of the lamella, in contact with it; a short, free horizontal plica is visible under the lamella; palatal wall with six plicae, first straight, last slightly curved, the middle plicae are divided in the middle, the fragments are horizontal, oblique or Z-shaped.

Differential diagnosis: *E. species8 u. sp.* is usually, larger, has domed dorsal surface, rounded body whorl and lack hairs standing in spiral rows. *E. species5 u. sp.* also has more elevated spire and more rounded body whorl. Moreover, *E. species5 u. sp.* has five rows of periostracal folds. *E. nomennovum1* is smaller and has weaker keeled body whorl, first and second rows of the periostracal folds are comparatively at larger distance than in *species4 u. sp.* Probably the most similar species is *E. pinacis*, which is nevertheless usually larger, has weaker keel and has well-visible spiral lines on the ventral side of the shell, which are missing in *E. species4 u. sp.*

Measurements (in mm): D: 8.5, H: 3.5; D: 5.5, H: 2.5, Wh: 5 (semiadult specimen).

shouldered/angulated body whorl of the new species.

Type locality: PL001 Nepal, Taubas, Bhainse, Makwanpur District., 27°49'25.21"N, 85°04'48.39"E.

Distribution: *E. species4* u. sp. is known from the type locality so far (Figure 7.121).

***Endothyrella babbagei* (Gude 1915)**

Figures 7.23, 7.30, 7.41

1915 *Plectopylis (Sinicola) babbagei* Gude: Records of the Indian Museum, 8: 512–513, plate 42, Figs 4a–d. ["Luyor Peak, Abor Hills, alt. 7200 ft. Lat. 28°45'. Long. 95°45'"]

1920 *Plectopylis (Sinicola) babbagei*, — Gude: Journal of Molluscan Studies, 14 (2–3): 64.

2013 *Endothyrella babbagei*, — Páll-Gergely & Hunyadi: Archiv für Molluskenkunde, 142 (1): 5.

Types: Peak Luyor, Abor Hills, 7,200 ft, leg. C. F. G. Oakes R. E., NHMUK 1903.7.1.3529. (holotype).

Diagnosis: A small (14 mm), dextral, widely umbilicated, flat species with hairs arranged in three spiral lines on the body whorl. Callus strong, palatal plicae short, simple, parietal wall with a single curved lamella.

Differential diagnosis: *E. babbagei* differs from the also dextral *E. oglei*, and *E. serica* by the flat dorsal side of the shell and the presence of hairs arranged in three lines along the body whorl. For differences with *E. species6* u. sp., see there.

Distribution: Only the holotype is known from the type locality (Figure 7.120).

***Endothyrella bedfordi* (Gude 1915)**

Figures 7.26, 7.41

1915 *Plectopylis (Chersaecia) bedfordi* Gude: Records of the Indian Museum, 8: 510–511, plate 42, Figs 2a–d.

["Abor country, Tsanspu Valley, on the Dihang, about 50 miles above the junction of the Sigon River, alt. 2800 ft."]

Types: Transpu Valley Abor Hills, 2800 ft, leg. C. F. G. Oakes R. E., NHMUK 1903.7.1.3584. (2 syntypes).

Diagnosis: A very small (ca. 9 mm), sinistral, brownish species with moderately wide umbilicus, almost flat dorsal surface (only the apex is elevated slightly), and rounded body whorl. Callus strong, palatal plicae long, more or less straight horizontal, with dichotomously divided posterior ends and many small denticles at their posterior ends; lamella single, curved, in contact with a lower plica, which runs until the peristome.

Differential diagnosis: *E. bedfordi* has a single curved parietal lamella with a long lower plica (which runs until the peristome) attached to it, and at the posterior ends of palatal plicae there are several small denticles. These features distinguish *E. bedfordi* from similar species.

Distribution: The species is known from the type locality only (approximately 28°44'N, 94°56'E) (Figure 7.122).

***Endothyrella blanda* (Gude 1898)**

Figures 7.27, 7.35, 7.41, 7.56, 7.97

1898b *Plectopylis blanda* Gude: Science Gossip, 4: 264, Figs 70 a–f. ["Naga Hills, Assam"]

1899e *Plectopylis (Endothyra) blanda*, — Gude: Science Gossip, 6: 148.

1899f *Plectopylis (Endothyra) blanda*, — Gude: Science Gossip, 6: 175, 176.

1900b *Plectopylis blanda*, — Gude: The Journal of Malacology, 7: 34–35, Figs 11a–f. ["Naga Hills, Assam"].

1914b *Plectopylis (Endothyra) blanda* (partim), — Gude: The Fauna of British India...: 73, 77–78, Figs 28a–f. ["Assam: Naga Hills"].

Types: Naga Hills, NHMUK 1922.8.29.41., coll. Godwin-Austen (holotype).

Museum material examined: Richila Peak, Sikkim, India, coll. Ottó, MMGY 66425/2; Damsang, coll. Godwin-Austen, NHMUK/26; Rissetchu, Sikkim, coll. Godwin-Austen, NHMUK/8; Rissetchu & Richila Peak, W. Bhutan, coll. Godwin-Austen, NHMUK/33 (several of these are juvenile shells); Sikkim, coll. Godwin-Austen, NHMUK (mixed sample with *E. nomennovum1*); Richila Peak, Sikkim, coll. Godwin-Austen, NHMUK/≈80; Risset-Chu, Sikkim, NHMUK/many shells; Sikkim, NHMUK/8; Sikkim (large variety), coll. Beddome ex coll. Godwin-Austen, NHMUK 1912.4.16.318/1; Sikkim, Rinkpo valley, NHMUK 1906.1.1.752/1; Sikkim, Rechila Peak, coll. W. Robert, NHMUK 1903.7.1.28/1; Sikkim, NHMUK/8; Sikkim, Rarhichu, coll. Godwin-Austen, (labelled as *hanleyi*?) NHMUK/1; Sikkim, Rarhichu, NHMUK (mixed sample with *E. nomennovum1*); Darjeeling, India, West Bengal, Darjeeling, North Point 900–1400 m asl., under stones in forest clearings, coll. Topál, 1967. HNHM 98849/2.

Diagnosis: A very small (ca. 6 mm), sinistral species with narrow umbilicus, conical dorsal surface and 7 rows of hairs. Callus weak but present; palatal plicae divided, posterior fractions denticle-like; anterior fractions horizontal, straight; lamella straight of very slightly S-shaped, with posterior denticles above and below, and with a lower and an upper plica close to the sutures.

Differential diagnosis: Species similar in size (*E. macromphalus*, *E. nomenovum*1) have depressed shell.

Moreover, *macromphalus* shells are smooth on the ventral side, whereas most *blanda* shells have hairs, or in case of corroded specimens, holes which indicate the hairs' positions. The most similar species in terms of shell shape and size is *E. williamsoni* which has two horizontal parietal plicae anterior to the lamella (these are missing in *E. blanda*).

Characters of the genital structure: Two specimens were anatomically examined. Collection data: Silchar Cachar, F. Ede, coll. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.502. Both specimens had several embryos developing in the uterus.

The left ommatophoral retractor passes between penis and vagina. Atrium short, penis long, rather cylindrical, but slowly tapers towards the distal end; opening the penis was very difficult, not only because of its size, but also due to the very old specimen; the internal morphology could hardly be seen, although parallel folds forming "pockets" were visible; a little thickening has been found near the posterior end of the penis, this could be interpreted as a penial caecum. The slender and relatively long retractor muscle inserts on the distal end of the penis, slightly in distal direction from the caecum; epiphallus also slender, slightly longer than the penis; vas deferens long and slim; vagina shorter than the penis and epiphallus combined, it is very thick, with a well-developed vaginal bulb; several short muscle fibres attaches the vagina to the body wall and diaphragm; both the gametolytic sac and the diverticulum are very long and slim, although the gametolytic sac is somewhat thickened.

Radula: Figure 7.97 and Table 7.4.

Distribution: See remarks (Figure 7.123).

Remarks: According to the original description (Gude 1898) the holotype was received from Godwin-Austen, and was collected in the Naga Hills. On the other hand, all other specimens which are very similar to the holotype are collected from the Sikkim area which lies approximately 600 km from the Naga Hills. I assume that the type locality is erroneous and the species inhabits the Sikkim Area only.

***Endothyrella brahma* (Godwin-Austen 1879a)**

Figures 7.26, 7.41

1879a *Helix* (*Plectopylis*) *brahma* Godwin-Austen: Journal of the Asiatic Society of Bengal, 48 (2): 3–4, plate 1, Fig. 3. ["near Brahmakund, eastern Assam, at 1,000 feet elevation"]

1887 *Helix* (*Plectopylis*) *brahma*, — Tryon: Manual of Conchology..., 2 (3) 164, plate 36, Figs 35–37.

["Brahmakund, Eastern Assam; alt. 1000 ft."]

1894 *Plectopylis brahma*, — Pilsbry: Manual of Conchology, 2 (9): 145.

1897k *Plectopylis brahma*, — Gude: Science Gossip, 4: 170–171, Figs 63a–c. ["Brahmakund, Eastern Assam"]

1899e *Plectopylis* (*Chersaecia*) *brahma*, — Gude: Science Gossip, 6: 148.

1899f *Plectopylis* (*Chersaecia*) *brahma*, — Gude: Science Gossip, 6: 175, 176.

1914b *Plectopylis* (*Chersaecia*) *brahma*, — Gude: The Fauna of British India...: 74, 113–114, 54a–c. ["Assam: Brahmakund"]

1915 *Plectopylis* (*Chersaecia*) *brahma*, — Gude: Records of the Indian Museum, 8: 509, 511.

1920 *Plectopylis* (*Chersaecia*) *brahma*, — Gude: Journal of Molluscan Studies, 14 (2–3): 63.

Types: Brahmakund, E. Assam, NHMUK 1903.7.1.751. (6 syntypes).

Material examined: Assam, leg. Hungerford, NHMUK 1891.3.17.362–364/3; Assam, Brahmakund, coll. Godwin-Austen, NHMUK/27 (several shells juvenile);

Diagnosis: A very small (ca. 8 mm), sinistral species with narrow umbilicus, depressed conical dorsal surface, and conspicuous radial sculpture without hairs. Callus very strong; palatal plicae short, straight, with many small denticles at their posterior ends, standing along a vertical line; lamella oblique, with three horizontal plicae anteriorly, the lowermost is in contact with the lower end of the lamella. Besides these anterior plicae, there is a short upper plica above the lamella, and long lower plica close to the lower suture, which runs until the aperture.

Differential diagnosis: *E. brahma* can be distinguished from all other *Endothyrella* species by the presence of three parallel, horizontal parietal plicae anterior to the lamella.

Distribution: The species is known from the type locality only (Figure 7.122).

Endothyrella species5 u. sp.

Figures 7.28, 7.40

Material: **PL002** Nepal, Suridobhan, Dolakha, 1023 m, 27.758852°N, 86.197894°E, leg. Budha, P., 03.02.2009., CDZMTU001 (Holotype), CDZMTU002 (2 paratypes=shells from the same locality); **PL011** Nepal, Bhorle, Dolakha, 800 m, 27.696652°N, 86.129583°E, leg. Budha, P., 03.02.2009., CDZMTU003 (12 paratypes=shells).

Diagnosis: A small *Endothyrella* species with rather conical dorsal part and slightly angulated body whorl with five rows of hairs. Parietal lamella simple with one or two denticles posteriorly and a plica below, middle palatal plicae divided or almost divided.

Description: Shell sinistral, with somewhat elevated spire and rather conical apical part; protoconch elevates from the dorsal surface; colour brownish or greyish; protoconch conspicuously large, consists of 2.25, 2.5 whorls, very finely, regularly ribbed; teleoconch with well-visible reticulated sculpture dominated by radial growth lines; sculpture somewhat weaker on the ventral surface; very slender, long periostracal folds (hairs) standing in five spiral lines along the body whorl; whorls 5.25–5.5 (n=3) moderately bulging, separated by relatively deep suture; umbilicus wide and deep; apertural lip whitish, thin, slightly reflexed; callus also very weak, slightly S-shaped; no fold in the aperture.

One specimen was opened (PL002). Parietal wall with one rather straight lamella with slight lower arms pointing in both directions; small denticle near the upper end posteriorly, connected to the lamella; two short horizontal plicae under the lamella; palatal wall with six plicae; first slim and short, the second-fifth plicae are divided in the middle and are of the same size; last plica also short, rather straight.

Differential diagnosis: *E. species5 u. sp.* differs from *E. species8 u. sp.* by the usually smaller size, fewer whorls, stronger sculpture, comparatively larger protoconch, conical apical part, slightly angulated body whorl and the presence of hairs standing in five spiral lines. The probably closest related species are *E. affinis* and *E. plectostoma*, which are larger, have higher spire, deeper and narrower umbilicus. *E. macromphalus* is hairless, has weaker sculpture, and its dorsal surface is not conical, but only the protoconch is elevated from the surface. *E. nomennovum1* is smaller, flatter has more elevated parietal callus, and has only four rows of hairs. See also under *E. species4 u. sp.*

Measurements (in mm): D= 6.5–9.0, H= 4.0–5.0. (n=5).

Type locality: Nepal, Suridobhan, Dolakha, 1023 m, 27.758852°N, 86.197894°E.

Distribution: *E. species5 u. sp.* is known from two nearby localities in the valley of the Tamakoshi River, central Nepal (Figure 7.121).

***Endothyrella fultoni* (Godwin-Austen 1892)**

Figures 7.28, 7.57, 7.93, 7.95, 7.107

1892 *Helix* (*Plectopylis*) *fultoni* Godwin-Austen: The Annals and Magazine of Natural History, 6 (10): 300–301.

["Exact locality unknown. Khasi Hills?"; detailed description on the exactness of the locality on page 301]

1893 *Plectopylis fultoni*, — Pilsbry: Manual of Conchology..., 2 (8): 296, 297.

1894 *Plectopylis fultoni*, — Pilsbry, Manual of Conchology..., 2 (9): 144, 146, plate 40, Figs 13–15.

1894–1895 *Plectopylis fultoni*, — Pilsbry, Manual of Conchology. Second Series: Pulmonata, Vol. 9: 296–297.

1896d *Plectopylis fultoni*, — Gude: Science Gossip, 3: 178–179, Figs 23a–b. ["the habitat of Khasi Hills, India, is doubtfully given, but the exact locality is unknown"]

1899e *Plectopylis* (*Endothyra*) *fultoni*, — Gude: Science Gossip, 6: 148.

1899f *Plectopylis* (*Endothyra*) *fultoni*, — Gude: Science Gossip, 6: 175, 176.

1914b *Plectopylis* (*Endothyra*) *fultoni*, — Gude: The Fauna of British India...: 72, 87–89, Figs 36a–b. ["Assam : Khasi Hills"]

Types: Khasi Hills (?) from Fulton, NHMUK 1903.7.1.301. (2 syntypes).

Museum material examined: Ost-Ind., coll. Gerstenbrandt, NHMW 5954/2; Khasi Hills, Assam, coll. Rušnov, ex coll. Blume, NHMW/1; Khasi Hills, leg. Godwin-Austen, NHMW 19599/2; India, Meghalaya, Khasi Hills, leg. Godwin-Austen, Altonaer Museum, ZMH 45907/2; Khasi-Berge, coll. Möllendorff, SMF 150103/3; Assam, Cherrapoonjeh, SMF 150104/4; Ostindien, Assam, coll. C. R. Boettger 1909, SMF 102818/1; Indien, Khasi Berge, coll. Dosch ex coll. Rolle, SMF 172070/3; Khasi Hills, Coll. Blanford, 1906.1.1.737/2; Khasi Hills, coll. Fulton, NHMUK/3; Assam, Khasi Hills, coll. Trechmann, NHMUK/2; Assam, Khasi Hills, NHMUK 1892.9.11.9–11/3; Assam, Khasi Hills, coll. Lucas, NHMUK/2; Assam, Khasi Hills, coll. Smith, NHMUK 1937.12.30.13862–13864/3;

India, Khasi Hills, coll. Salisbury ex coll. Beddome, NHMUK/2; Khasi Hills, Assam, coll. Gude, coll. Kennard, NHMUK/9; Assam, Cherrapunje, coll. Lucas, NHMUK/1; no locality, dissected dried animal, NHMUK/3;

Diagnosis: A middle sized to large (18–20 mm), sinistral species with trapezoid shell, narrow umbilicus, angled body whorl, an apex which is elevated from the dorsal surface, and four rows of hairs on the body whorls. Callus very strong; 3rd, 4th and 5th palatal plicae are divided in the middle, the others are more or less straight and horizontal; lamella vertical or oblique, with short lower and upper plicae above and below.

Differential diagnosis: *E. fultoni* is much larger than any other *Endothyrella* species and has a characteristic reversed trapezoid shell shape.

Characters of the genital structure: A single specimen was anatomically examined. Collection data: Khasi, leg. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.598. The specimen had some embryos developing in the uterus. The whole body was very fragile, therefore the gametolytic sac and the additional organ next to it could not be dissected out.

The left ommatophoral retractor passes between penis and vagina. Atrium relatively long; penis long, consists of a longer, slimmer proximal and a shorter, more thickened distal part; at the distal end of the penis there is a rounded thickening; penis internally with honey-comb-like tubercles without calcareous granules; the somewhat slimmer penial caecum has some (approximately 8) parallel folds inside, which also form minute hollows standing in lines between the folds; these small pockets may also serve for small calcareous granules; epiphallus enters penis at the basis of the rounded penial thickening; epiphallus relatively short, approximately as long as the distal, thickened part of the penis; retractor muscle inserts on the distal end of the penial caecum, it is approximately as long as the distal part of the penis; vas deferens long and thick, it becomes curly near its insertion to the spermoviductus; vagina shorter than the the half of the penis; it has a vaginal bulb at the middle; two fascia of fibres attach the distal and proximal part of the vaginal bulb to the body wall; there are also some single, longer and more slender muscle fibres attached to the vagina; gametolytic sac relatively thick, the additional organ next to it is more slender.

Radula: Figure 7.107 and Table 7.4.

Distribution: The species is assumed to be lived in the Khasi hills (see Godwin-Austen 1892) (Figure 7.123).

Endothyrella hanleyi (Godwin-Austen 1879b)

1879b *Plectopylis hanleyi* Godwin-Austen: The Annals and Magazine of Natural History, 5 (4): 164. ["Sikkim?"]

1897f *Plectopylis hanleyi*, — Gude: Science Gossip, 4: 11.

1899a *Plectopylis hanleyi*, — Gude: Science Gossip, 5: 240. ["Sikkim?"]

1899e *Plectopylis (Endothyra) hanleyi*, — Gude: Science Gossip, 6: 148.

1899f *Plectopylis (Endothyra) hanleyi*, — Gude: Science Gossip, 6: 175, 176.

1914b *Plectopylis (Endothyra) hanleyi*, — Gude: The Fauna of British India... : 73, 77. ["Sikkim?"]

Remarks: In the original description Godwin-Austen wrote that the holotype is "in the collection of Mr. Sylvanus Hanley". In Godwin-Austen's copy of Gude (1914, page 77), Godwin-Austen has written "In my collection".

The original type specimen was not found in the collection of the NHMUK. Only one specimen was assigned to *Plectopylis hanleyi*, marked the determination with a question mark ("Sikkim, Rarhichu, H. H. Godwin-Austen colln.") (handwriting of whom?). This specimen however is very similar to the type specimen of *Plectopylis blanda*, and not identical with the single shell in Godwin-Austen's (1879b) description, because its spire is rather raised (in the description it is "depressedly conoid"), it has 4.75 whorls (the holotype has 6) and moreover, Godwin-Austen (1879b) described the palatal lamellation, whereas our specimen is intact, therefore the inner lamellae and plicae could not be observed.

Endothyrella species6, n. sp.

Figures 7.27, 7.30, 7.34, 7.40

Material: China, Sichuan Sheng, Panzhihua Shi, Yanbian Xian, Qinghe Xiang, Qinghepubu, Xianrendong, 1410 m, 27°03.834'N, 101°23.611'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 12.09.2013, NHMUK 20140023 (holotype), JUO/1 (paratype), TH/1 (paratype=juvenile shell); China, Sichuan Sheng, Liangshan Yizu Zizhizhou, Yanyuan Xian, Bainiao Zhen, Kedengrongdong (cave), 2620 m, 27°43.103'N, 101°31.021'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 13.09.2013, JUO/1 juvenile shell (not paratype).

Diagnosis: A small, dextral species with elevated callus, hairs standing in three lines on the body whorl, a single, curved lamella on the parietal and six short plicae on the palatal wall.

Description: Shell dextral, almost flat, with very slightly domed apical part; protoconch slightly elevated from the dorsal surface; brownish or slightly reddish; protoconch consists of 1.5–1.75 whorls, first whorls rather smooth, last 0.25–0.5 whorl regularly ribbed; teleoconch with irregular, rough growth lines and spiral structure; sculpture stronger on the dorsal side but still well-visible on the ventral surface; deciduous, slim and flat folds standing in three lines on the body whorl; whorls 4.75, very much bulging, separated by deep suture; umbilicus moderately wide and deep; apertural lip whitish, thickened and slightly reflexed; callus strong, elevated, sharp and slightly S-shaped; with canals at both ends; no fold in the aperture.

One specimen (the holotype) was opened. Armature is situated very close to the aperture, palatal plicae visible from oblique view through the aperture. Parietal wall with a single curved lamella without additional denticles; arms of the lamella pointing posteriorly; palatal wall with six very short plicae becoming narrower posteriorly; the last one with an additional denticle posteriorly.

Differential diagnosis: *E. babbagei* is much larger, has flatter whorls and has weaker callus. The other dextral *Endothyrella* species (*oglei*, *serica*) have elevated spire and narrower umbilicus and the periostracal folds on the body whorl are missing. *Sinicola* species of the same size have keeled or shouldered body whorl and they have two parallel parietal plicae anterior to or above the lamella (one near the upper, the other near the lower suture). *Sicradiscus invius* also lives in Sichuan, but it is smooth and has a strong apertural fold.

Measurements (in mm): D= 6.6–6.7, H= 3.0–3.1 (n=2, from different localities).

Type locality: China, Sichuan Sheng, Panzhihua Shi, Yanbian Xian, Qinghe Xiang, Qinghepubu, Xianrendong, 1410 m, 27°03.834'N, 101°23.611'E.

Distribution: *E. species6* u. sp. is known from two localities in western Sichuan province, China (Figure 7.120).

***Endothyrella species7* u. sp.**

Figures 7.22, 7.40

1914b *Plectopylis (Endothyra) blanda* (partim), — Gude: The Fauna of British India... : 73, 77–78, Figs 28a–f. ["Assam: Naga Hills"].

Material: Naga Hills, Ihang valley, coll., Godwin-Austen, NHMUK 1903.7.1.770/3; Manipur, Laisen Peak, coll. Godwin-Austen, NHMUK 1903.7.1.3453/1; Naga Hills, coll. Godwin-Austen, NHMUK 1903.7.1.767/3; Lhota Naga Hills, coll. Chennell, NHMUK 1903.7.1.765/4.

Diagnosis: A very small species with elevated spire, smooth ventral side and strongly reticulated dorsal side.

Description: Shell sinistral, with slightly elevated spire and conical/domed apical part; colour light brown, greenish or yellowish; protoconch consists of approx. 2 whorls, glossy, in some populations (NHMUK 1903.7.1.767, NHMUK 1903.7.1.770, NHMUK 1903.7.1.3453) only the last half whorl has somewhat ribbed surface, whereas in others (NHMUK 1903.7.1.765) nearly the whole protoconch was ribbed; dorsal side of the teleoconch with well-visible reticulated sculpture dominated by spiral lines; ventral side hairless, smooth, glossy, sometimes with radial growth lines; the ventral and dorsal surface change relatively abruptly above the middle line of the body whorls (from apertural view); inside the umbilicus there are sharp periostracal folds corresponding with radial ribs; whorls 4.5–4.75 (n=3), slowly growing, separated by relatively deep suture; umbilicus narrow and deep; apertural lip whitish, thickened, normally not reflexed, or reflexed only near the umbilicus; callus very weak, nearly not visible in case of fresh shells, in case of old, corroded shells it becomes white; aperture without entering fold.

Two opened specimens were observed (NHMUK 1903.7.1.767 and NHMUK 1903.7.1.765). Parietal wall with one rather straight lamella which bents anteriorly; it has both the upper and lower ends elongated anteriorly; two small denticles visible at the posterior side of the lamella, one above and one below; upper plica absent, lower plica very long, reaches the peristome; palatal wall with six plicae; first slim and short, the second-fifth plicae rather straight, horizontal; they do not seem to be divided if we observe through the translucent shell wall, but their middle portion (where the lamella is present on the parietal wall) is much lower; the posterior ends of the middle plicae slightly bent downwards; the last plica is short and slightly curved.

Differential diagnosis: *E. blanda* is similar in shells shape to *E. species7* u. sp., but is larger, has hairy ventral surface (or if hairs are missing, than hollows indicating the hairs' position are visible), and on its dorsal surface the radial lines are dominant. *E. williamsoni* is also larger, and has a long main plica on the parietal wall which is missing in *E. species7* u. sp. *E. macromphalus* is larger, has wide umbilicus and depressed spire. *E. nomennovum1* is entirely flat and has hairy ventral surface.

Measurements (in mm): D= 4.1–4.6, H=2.3–3.5, n=2 (NHMUK 1903.7.1.765).

Distribution: The new species is known only from the Naga Hills and Manipur (Figure 7.123).

***Endothyrella macromphalus* (W. Blanford 1870)**

Diagnosis: A very small (ca. 6–8.5 mm), sinistral species with relatively wide umbilicus, reticulated, almost flat dorsal surface (only the apex is elevated) and smooth ventral side. Callus weak, only very slight whitish lime layer is visible; palatal plicae straight, divided or not, lamella with short upper and lower plicae and two posterior denticles, one above and one below.

Differential diagnosis: See under *E. blanda* and *E. williamsoni*.

Remarks: The type specimen of *Plectopylis gregorsoni* is very similar to typical *E. macromphalus* specimens. The only difference is that the palatal plicae are not divided in *gregorsoni*. In my view this minor difference is not sufficient for species level distinction; therefore I refer to *Plectopylis gregorsoni* as the subspecies of *Endothyrella macromphalus*.

***Endothyrella macromphalus macromphalus* (W. Blanford 1870)**

Figure 7.27

- 1870 *Helix* (*Plectopylis*) *macromphalus* Blanford: Journal of the Asiatic Society of Bengal, 39 (2): 17–18, plate 3, Fig. 14. ["ad Mairung in montibus Khasi"]
- 1870–1876 *Helix macromphalus*, — Hanley & Theobald: Conchologia Indica...: plate 83, Figs 8–10.
- 1875b *Plectopylis macromphalus*, — Godwin-Austen: Proceedings of the Zoological Society of London: 612, 613, plate 73, Figs 1, 1a. ["Darjeeling and N. E. frontier, Bengal. Khási"]
- 1878a *Helix* (*Plectopylis*) *macromphalus*, — Nevill: Hand list of Mollusca in the Indian Museum, Calcutta...: 71.
- 1879b *Helix* (*Plectopylis*) *macromphalus*, — Godwin-Austen: The Annals and Magazine of Natural History, 5 (4): 163–164.
- 1887 *Helix* (*Plectopylis*) *macromphalus*, — Tryon: Manual of Conchology..., 2 (3): 160, plate 34, Figs 65–68. ["Khasi Mts. and near Darjiling, India"]
- 1892 *Plectopylis macromphalus*, — Godwin-Austen: The Annals and Magazine of Natural History, 6 (10): 301.
- 1893 *Plectopylis macromphalus*, — Pilsbry: Manual of Conchology..., 2 (8): 297.
- 1894 *Plectopylis macromphalus*, — Pilsbry: Manual of Conchology..., 2 (9): 146.
- 1897f *Plectopylis macromphalus*, — Gude: Science Gossip, 4: 10–11, Figs 46 a–b. ["Khasia, Dafla and Naga Hills, in Assam"]
- 1899e *Plectopylis* (*Endothyra*) *macromphalus*, — Gude: Science Gossip, 6: 147, 148.
- 1899f *Plectopylis* (*Endothyra*) *macromphalus*, — Gude: Science Gossip, 6: 175, 177.
- 1914b *Plectopylis* (*Endothyra*) *macromphalus*, — Gude: The Fauna of British India...: 72, 79, Figs 29a–b. ["Assam: Mairung, Khasi Hills", "Dafla Hills", "Naga Hills"]
- 1915 *Plectopylis* (*Endothyra*) *macromphalus*, — Gude: Records of the Indian Museum, 8: 507.

Types: Darjiling, coll. W. Blanford, NHMUK 1906.1.1.754. (holotype).

Material examined: Khasi Berge, SMF 150102/3 (mixed sample with *E. nomemnovum*1); Khasi Berge, coll. Dosch, ex coll. Rolle, SMF 172069/2; Dafla Hills, Burreil Gorge, coll. Godwin-Austen, NHMUK 1903.7.1.772/11; Khasi Hills, Mairang, coll. Blanford, NHMUK 1906.2.2.362/4; Khasi Hills, coll. Godwin-Austen, Figured in Godwin-Austen (1874), NHMUK 1903.7.1.766/9; Mairang, Khasi, NHMUK 1906.1.1.750/1; India, NHMUK 41.9.28.68/4; no locality, NHMUK/approx.70; Digny, coll. Godwin-Austen, NHMUK/1; Shillong, Khasi, animal dissected, NHMUK 1903.7.1.773/1; Teria Ghat, coll. Godwin-Austen, NHMUK/1; Brit. Indien, Toruputu Dfola, 5000', coll. Ehrdmann ex coll. Webb, SMF 150101/3.

Differential diagnosis: See under *E. macromphalus gregorsoni*.

Distribution: *E. macromphalus* seems to have a wide range including Assam and the Dafla and Khasi Hills. It has been reported from the Naga Hills, but those samples are probably misidentified (Figure 7.123).

***Endothyrella macromphalus gregorsoni* (Gude 1915)**

Figure 7.27

- 1915 *Plectopylis* (*Endothyra*) *gregorsoni* Gude: Records of the Indian Museum, 8: 506–507, plate 41, Figs 2a–d. ["Yamne Valley, Abor Hills"]

Types: Yamne Valley, Abor Hills, leg. C.F.G. Oakes, R.E., NHMUK 1903.7.1.3124.

Differential diagnosis: The nominotypical subspecies has divided palatal plicae, which are not divided in *G. macromphalus gregorsoni*.

Distribution: *Endothyrella macromphalus gregorsoni* is recorded from the type locality only (approximately: 28°13.4'N, 95°13.3'E) (Figure 7.123).

***Endothyrella miriensis* (Gude 1915)**

Figure 7.28

1915 *Plectopylis (Endothyra) miriensis* Gude: Records of the Indian Museum, 8: 507–508, plate 41, Figs 3a–d. ["Miri Hills, Upper Assam"]

Types: Miri Hills, leg. C.F.G. Oakes, R.E., NHMUK 1903.7.1.3205. (4 syntypes)

Diagnosis: A small (ca. 12 mm), sinistral species with very slightly elevated spire, relatively wide umbilicus, and conspicuous spiral sculpture. Callus moderately strong, palatal plicae slightly oblique, they are connected by a vertical ridge; lamella almost straight, with anteriorly elongated upper and lower ends and small denticles on the posterior side, one above and one below.

Differential diagnosis: The unique spiral sculpture distinguishes *E. miriensis* from all congeners.

Distribution: The species is known from the type locality only (Figure 7.122).

Endothyrella species8 u. sp.

Figures 7.25, 7.30, 7.34, 7.40, 7.58

Material: W-Nepal, Dhaulagiri Zone, Myagdi District., Annapurna Conservation Area, right side of Kali Gandaki valley, 300 m NNW of Suke Bagar village along "Tatopani-Dana" track, 1430 m alt., 14.05.1996., leg. A. Kuznetsov, WM/10 paratypes; Nepal, Kathmandu Valley, NW end of Kathmandu, middle part of S slope of Swoyambhunath Hill, in dry oak forest, 1500 m, 25.04.1995, leg. A. Kuznetsov, WM/4 sinistral and 1 dextral paratypes; **PL003** Nepal, Swoyambhunath, Kathmandu District, 1366 m, 27.716971N, 85.289386 E, leg. Budha, P., 05.09.2008, CDZMTU006 (22 paratypes=shells), PGB/2 paratypes; **PL004** Siddhacave, Tanahun District, 600 m, 27.94718°N, 84.421338°E, leg. Budha, P., 24.10.2008, CDZMTU004, CDZMTU007 (10 paratypes=shells), PGB/1 paratype and one juvenile shell (not paratype); **PL005** Dhunche, Rasuwa, 1985 m, 28.1092°N, 85.2916°E, leg. Budha, P., 31.05.2007., CDZMTU008 (Paratypes= 1 shell), PGB/1 paratype and one damaged shell (not paratype); **PL006** Champadevi, Kirtipur, Kathmandu District 1326–1500 m, 27.654868°N, 85.244084°E, leg. Budha, P., 02.10.2010., holotype (CDZMTU005.1), paratypes CDZMTU005.2–16 (15 shells), CDZMTU005P (2 paratypes=specimens dissected and preserved), PGB/3 paratypes and 2 juvenile shells (not paratypes); **PL007** Balaju, Kathmandu District, 1356 m, 27.741173°N, 85.293763°E, leg. Budha, P., 04.01.2009., CDZMTU009 (8 paratypes=shells), CDZMTU009P (2 paratypes=specimens preserved), PGB/4; **PL008** Mahadevsthan, Thankot, Kathmandu District 1500 m, 27.683366°N, 85.213834°E, leg. Budha, P., 06.02.2007., CDZMTU010 (25 paratypes=shells), CDZMTU010P (2 paratypes=specimens preserved), PGB/4 paratypes and 5 juvenile shells (not paratypes); **PL009** Arjewa, Baglung, 900 m, 28.154393°N, 83.630703°E, leg. Budha, P., 13.09.2006., CDZMTU011 (10 paratypes=shells), PGB/4 paratypes and one juvenile shell (not paratype); **PL010** Majhbeni, Parbat, 700 m, 28.205708°N, 83.674605°E, leg. Budha, P., 13.09.2006., CDZMTU012 (5 paratypes=shells), PGB/4 paratypes and 6 juvenile/damaged shells (not paratypes); **PL012** Sirsuwa, Parbat District, 780 m, 28.136478°N, 83.642135°E, leg. Budha, P., 13.09.2006., CDZMTU013 (4 paratypes=shells), PGB/2 paratypes; **PL013** Foksing, Parbat District, 790 m, 28.093252°N, 83.604283°E, leg. Budha, P., 11.06.2006., CDZMTU014 (8 paratypes=shells), PGB/3 paratypes and 2 juvenile shells (not paratypes); **PL014** Godawari, Lalitpur, 1868 m, 27.94718°N, 84.421338°E, leg. Budha, P., 01.10.2008., CDZMTU015a (1 paratype); **no code** Annapurna Conservation Area, Tatopani, 1282 m, 28.495172°N, 83.628883°E, leg. Budha, P., 01.10.2008., CDZMTU016 2 (2 paratypes=shells); **no code** Godawari, Lalitpur, 1575 m, 27.596459°N, 85.389432°E, leg. Budha, P., 30.06.2007., CDZMTU015b (1 paratype=shell); **no code** Ridi, Gulmi, 832 m, 27.945621°N, 83.43215°E, leg. Budha, P., 30.06.2007., CDZMTU017 (5 paratypes=shells); **no code** Godawari Botanical Garden, Lalitpur, 1453 m, 27.596671°N, 85.381758°E, leg. Budha, P., 03.09.2008., CDZMTU015c (50 paratypes=shells); Nepal, Pokhara, Kaare, 1520 m alt., 28.2860°N, 83.8472°E, leg. C. Huber, 18.03.1991, NMBE 527538/1.

Diagnosis: A small or middle-sized, hairless species with domed dorsal part and rounded body whorl. Parietal lamella simple with one or two denticles posteriorly and sometimes a plica below the lamella, middle palatal plicae divided or almost divided.

Description: Shell sinistral, with somewhat elevated spire and domed apical part; protoconch slightly elevates from the dorsal surface; usually brownish but sometimes turns into yellowish; protoconch consists of 1.5–1.75 whorls, very finely, regularly ribbed; teleoconch with very weak, irregular growth lines on the ventral surface and fine reticulated sculpture on the dorsal side; in high magnification the surface is covered by flat periostracal folds; no spirally arranged large deciduous folds found; whorls 5.5–6.25, moderately bulging, separated by relatively deep suture; umbilicus wide and deep, whorls almost flat inside, resulting in an infundibular shape, apertural lip whitish, rather thin, slightly reflexed; callus inconspicuous, but present, slightly S-shaped; no fold in the aperture.

More than ten specimens were opened from different populations. One slightly curved lamella ornaments the parietal wall with arms pointing in the direction of the aperture; lower end more conspicuously curved; two small denticles above and below posteriorly of the lamella (the lower one is exceptionally missing); in some populations (e.g. PL010, PL006, PL004) with short plica under the lamella; palatal wall with six plicae; first slim and short, parallel with the suture; second plica is the longest, it shows a tendency towards dividing in the middle, but the two parts always fused; third, fourth and fifth plicae usually divided (third one sometimes not); last plica short, slightly curved with arms pointing in the direction of the lower suture.

Differential diagnosis: The most similar species is *E. pinacis*, which nevertheless has lower spire and shouldered whorls, whereas *Endothyrella* species8 u. sp. has rounded whorls and domed apical part. The ventral surface of the two species is similar, but *E. pinacis* has slender hairs standing in 3 lines, which is missing in *E. species8 u. sp.* According to previous studies (Godwin-Austen 1889–1914, Schileyko 1999) *E. pinacis* has no additional organ parallel with the gametolytic sac, but in all *E. species8 u. sp.* we dissected that organ was present. For comparison with *E. oakesi* and *E. species5 u. sp.*, see there.

Measurements (in mm): D= 8.2–14.9, H= 4.0–6.0, Wh= 5.5–7.5 (n=35, shells belonging to different populations).

Characters of the genital structure: Penis short, narrow proximally and slowly tapers toward the distal end; internal surface with several tubercles including minute calcareous hooks; epiphallus slender, cylindrical, longer than the penis; penial caecum very short, blunt, cylindrical, with a short retractor muscle attached at its distal end; vas deferens thin and nearly 1.5 times longer than epiphallus, convoluted before connection to prostate; vagina shorter than the penis with well-developed vaginal bulb; gametolytic sac very thin throughout and ends into a small rounded sac; there is an additional, slender organ with unknown homology running parallel with the gametolytic sac; it is as long as the gametolytic sac.

Type locality: Champadevi, Kirtipur, Kathmandu District, 1326–1500 m, 27.654868°N, 85.244084°E.

Distribution: *E. species8 u. sp.* inhabits a relatively large area in western and Central Nepal (Figure 7.121).

Remarks: Schileyko (1999) figured a shell from the "SW slope of Swayambhunat hill, Kathmandu valley, Nepal" (Figure 594.). The figured specimen is probably *Endothyrella* species8 u. sp., which inhabits the named area, but the drawing is not sufficient for identification.

Endothyrella oakesi (Gude 1915)

Figure 7.26

1915 *Plectopylis (Endothyra) oakesi* Gude: Records of the Indian Museum, 8: 505–506, plate 41, Figs 1a–d. ["Yamne Valley, Abor Hills and Sibbum", "between Riu and Singging, on the Dihang River"].

Types: Yamne Valley, Abor Hills, leg. C.F.G. Oakes, R.E., NHMUK 1903.7.1.3125. (5 syntypes).

Material examined: Sibbum, Abor, NHMUK, coll. Godwin-Austen, NHMUK/1; Abor Hills, "exact position not known", below alt. 3000' between lat. 28°15'+29°15', long. 94°50'+95°10', leg. Oakes, coll. Godwin-Austen, NHMUK 1903.7.1.3125/1;

Diagnosis: A small (ca. 12.5 mm), sinistral species with wide umbilicus, and slightly domed dorsal surface. Callus strong, palatal plicae complicated, their anterior part is horizontal, but the posterior part vertical, and there are several short horizontal plicae between them; lamella almost straight with posteriorly elongated upper end, and sometimes with a long lower plica which reaches the aperture.

Differential diagnosis: Similar to *P. pinacis*, but has much more complicated palatal plicae, more descending aperture, differently shaped umbilicus and more rounded body whorl. *E. species8 u. sp.* also has simpler palatal plicae than those of *E. oakesi*. Moreover, *E. species8 u. sp.* has flatter shell and less descending aperture.

Distribution: The species was reported only from the localities mentioned in the original description (Figure 7.122).

Remarks: Three specimens (two adults and a juvenile) of the type lot of *E. oakesi* were opened (probably by Gude). The long lower parietal plica, described as characteristic feature of this species, is present only in one specimen.

***Endothyrella oglei* (Godwin-Austen, 1879)**

Figures 7.23, 7.30

- 1879a *Helix* (*Plectopylis*) *Oglei* Godwin-Austen: Journal of the Asiatic Society of Bengal, 48 (2): 3, plate 1, Figs 2, 2a–c. ["Near Sadiya, Assam"]
1887 *Helix* (*Plectopylis*) *oglei*, — Tryon: Manual of Conchology..., 2 (3): 159, plate 36, Figs 29–31. ["Near Sadiya, Assam"]
1898b *Plectopylis oglei*, — Gude: Science Gossip, 4: 263, Figs 68a–h.
1899e *Plectopylis* (*Chersaecia*) *oglei*, — Gude: Science Gossip, 6: 148.
1899f *Plectopylis* (*Chersaecia*) *oglei*, — Gude: Science Gossip, 6: 175, 176.
1914b *Plectopylis* (*Chersaecia*) *oglei*, — Gude: The Fauna of British India...: 73, 92–93, Figs 39a–h. ["Assam, Sadiya"]

Types: Sadiya, E. Assam, leg. Ogle, NHMUK 1903.7.1.740. (4 syntypes).

Diagnosis: A small to middle sized (15–16 mm), dextral, yellowish-reddish striped species with moderately wide umbilicus and somewhat domed dorsal surface. Callus strong, palatal plicae divided at their middle and the posterior fragments are connected by a ridge; parietal wall with a single curved lamella with posteriorly elongated upper and lower ends. Probably at least the upper elongation is a denticle which fuses to the lamella.

Differential diagnosis: *E. oglei* differs from the also dextral *E. serica* by the much larger size, the absence of the groove on the protoconch which runs parallel with the suture in *E. serica*, and the morphology of the lamella which has only posteriorly elongated ends. For differences with the also dextral *E. babbagei* and *E. species6* u. sp., see under those species.

Distribution: The species is known from the type locality only (Figure 7.122).

Remarks: The information published by Gude (1914b) (major diameter 27, minor diameter 25 mm) is wrong; it probably refers to "*Chersaecia andersoni*."

***Endothyrella pinacis* (Benson 1859)**

Figures 7.25, 7.41

- 1859b *Helix pinacis* Benson: Annals and Magazine of Natural History, 3 (3): 268–269. ["Habitat raro in regione Sikkim in valle Rungun (4000 ped.), necnon prope Pankabari (1000 ped. alt.)"]
1860a *Helix* (*Plectopylis*) *pinacis*, — Benson: Annals and Magazine of Natural History, 3 (5): 243–247. ["Darjiling and the Khasia Hills"]
1868 *Helix pinacis*, — Pfeiffer: Monographia Heliceorum Viventium..., 5: 417. ["Darjiling et in montibus Khasia dictis"]
1868 *Helix* (*Corilla*) *pettos* Martens: Malakozoologische Blätter, 15: 158.
1869 *Helix pettos*, — Pfeiffer: Novitates conchologicae..., 462–463.
1872 *Helix pinacis*, — Hanley & Theobald: Conchologia Indica...: 7, 36, plate 13, Fig. 5, plate 84, Figs 1–4. ["Sikkim (Rungun, and near Pankabari)"]
1875b *Plectopylis pettos*, — Godwin-Austen: Proceedings of the Zoological Society of London, 612. ["Himalaya?"]
1875b *Helix* (*Plectopylis*) *pinacis*, — Godwin-Austen: Proceedings of the Zoological Society of London: 612, 613, plate 74, Fig. 1. ["Himalaya"]
1878a *Helix* (*Plectopylis*) *pinacis*, — Nevill: Hand list of Mollusca in the Indian Museum...: 71. ["Darjeeling"]
1879b *Helix* (*Plectopylis*) *pinacis*, — Godwin-Austen: The Annals and Magazine of Natural History, 5 (4): 163.
1887 *Helix* (*Atopa*) *pettos*, — Tryon: Manual of Conchology..., 2 (3): 156, plate 34, Figs 36–38. ["Himalaya Mts India"]
1887 *Helix* (*Plectopylis*) *pinacis*, — Tryon: Manual of Conchology... 2 (3) 159–160, plate 34, Figs 53–55. ["Sikkim region, Himalayas, India"]
1894 *Plectopylis pinacis*, — Pilsbry: Manual of Conchology..., 2 (9): 144, 146.
1894 *Plectopylis pettos*, — Pilsbry: Manual of Conchology..., 2 (9): 146.
1895 *Plectopylis pinacis*, — Godwin-Austen: Journal of the Asiatic Society of Bengal, 64: 154, plate 7, Figs 2, 2a.
1897a *Plectopylis pinacis*, — Gude: Science Gossip, 3: 206, Figs 32a–d. ["Sikkim"]

- 1897a *Helix (Corilla) pettos* = *Plectopylis pinacis*, — Gude: Science Gossip, 3: 206.
 1899e *Plectopylis (Endothyra) pinacis*, — Gude: Science Gossip, 6: 147, 148.
 1899e *Plectopylis (Endothyra) pettos* (under *pinacis*), — Gude: Science Gossip, 6: 148.
 1899f *Plectopylis (Endothyra) pinacis*, — Gude: Science Gossip, 6: 175, 177.
 1899f *pettos*, — Gude: Science Gossip, 6: 177.
 1907 *Plectopylis pinacis*, — Godwin-Austen: Land and freshwater Mollusca of India... : 203–204.
 1914b *Plectopylis (Endothyra) pinacis*, — Gude: The Fauna of British India... , 72, 86–87, Figs 35a–d. ["Sikkim : Darjeeling", "Rungun, Pankabari", "Rungmaval", "Damsang"]
 1914b *Plectopylis (Endothyra) pinacis*, — Gude: The Fauna of British India... : 72, 86.
 1915 *Plectopylis (Endothyra) pinacis*, — Gude: Records of the Indian Museum, 8: 506, 508.

Types: Sikkim, coll. Benson, UMZC 102755; Himalaya, ZMB/MOLL 17905 (holotype of *Helix pettos*).

Museum material examined: Darjiling, coll. Dr. Stoliczka, 1880, NHMW/7; Sikkim, coll. Möllendorff, SMF 150110/6 (3 of them juvenile); Darjeeling, coll. Dosch, ex coll. Rolle, SMF 172075/2; Darjiling, figured in Godwin-Austen (1874), coll. Godwin-Austen, NHMUK 1903.7.1.746/5; Darjiling, coll. Blanford, NHMUK 60.6.27.14/1; Kungna val. (?) Sik., NHMUK/2; Darjiling, NHMUK/ 1906.2.2.143/2; Damsang Peak, Daling Hills, coll. Godwin-Austen, NHMUK/26 (several of the juvenile); Sikkim, Rarkichu, NHMUK/5; Rarkichu, Sikkim, coll. Godwin-Austen, NHMUK/1; Rechila Peak, coll. Godwin-Austen, NHMUK/1; Darjiling, NHMUK 88.12.4.1524/1; Darjeeling, 5000', coll. Everest Expedition 1924, NHMUK/1; India, West Bengal, Darjeeling District, Lopchu+Ghum, coll. Topál, 21–22.04.1967, locality code: 869, HNHM 98848/2.

Diagnosis: A small to middle sized (ca. 14–15 mm), hairless sinistral species with wide umbilicus and slightly angulated body whorl. Callus strong, palatal plicae short and oblique, lamella rather straight with anteriorly elongated upper and lower ends, and posteriorly elongated upper end. There are two denticles on the posterior side of the lamella, one above and one below, the lower one might be in contact with the lamella.

Differential diagnosis: See under *E. species8* u. sp. and *E. species4* u. sp.

Characters of the genital structure: The anatomy of *Endothyrella pinacis* was described by Godwin-Austen (1889–1914) and Schileyko (1999). According to these descriptions, only the gametolytic sac is present and the diverticulum is missing. The other interesting thing is that the penial caecum seems to be missing, although any of these drawings show this part clearly. Other features of the genitalia (penis shape, internal wall of the penis, vagina) are similar to those of the other members of the genus.

Radula: Stoliczka (1871) mentioned that the central tooth is larger than that of *Plectopylis achatina* (= *bensoni*), and it has similar shape to that of the laterals. Godwin-Austen (1889–1914) gave an accurate description and drawings of the teeth. According to his drawings the morphology of the teeth of *E. pinacis* is typical to that of the genus *Endothyrella*. Namely, the central tooth is larger than the ectocones of the first laterals, and the marginals are tricuspid with deep incisions between the two innermost cusps.

Distribution: All museum samples I examined were collected from Sikkim. Benson's (1860) locality in the Khasi Hills is probably incorrect (Figure 7.123).

***Endothyrella plectostoma* (Benson 1836)**

Diagnosis: A small (8–10 mm), sinistral species with narrow umbilicus, conical dorsal surface, and hairs standing in five rows on the body whorl. Palatal plicae more or less straight, the 4th and 5th divided; lamella slightly curved, with short lower and long upper elongation in anterior direction. There are two denticles posteriorly, one above and one below.

Differential diagnosis: See under *E. affinis* and *E. sowerbyi*.

***Endothyrella plectostoma plectostoma* (Benson 1836)**

Figures 7.24, 7.34, 7.35, 7.41, 7.59, 7.93, 7.107

1836 *Helix (Helicodonta) plectostoma*, — Benson: Journal of the Asiatic Society of Bengal, 5: 351.

1848 *Helix plectostoma*, — Pfeiffer, Mart. & Chemnitz, 1(12): 367, pl. 64, Figs 19–21.

1854 *Helix plectostoma*, — Reeve: Conchologia iconica 7, species 782.

1860b *Helix plectostoma*, — Benson: Annals and Magazine of Natural History, 3 (5): 247.

- 1865 *Helix plectostoma*, — Blanford, Journal of the Asiatic Society of Bengal 34 (2): 94. ["...the Himalayan and Khasi *H. plectostoma*, Bens. abounded south of the town of Bassein in several places, Pyema Khyoung, Long Island, &c. It was also found by Captain Ingram in Arakan, near Tongoop."]
- 1872 *Helix (Plectopylis) plectostoma*, — Hanley & Theobald: Conchologia Indica...: 7, plate 13, Fig. 2. ["Darjiling and Khasia Hills"]
- 1875b *Plectopylis plectostoma*, — Godwin-Austen: Proceedings of the Zoological Society of London: 612–613, plate 73, Figs 2–2a. ["Darjeeling and N. E. frontier, Bengal"]
- 1878a *Helix (Plectopylis) plectostoma*, — Nevill: Hand list of Mollusca in the Indian Museum...: 1: 71. ["Nágá Hills", "Bassein, &c., Pegu", "Sylhet", "Arakan Hills", "Khasi Hills", "Darjeeling"]
- 1887 *Helix (Plectopylis) plectostoma*, — Tryon: Manual of Conchology...: 2 (3): 160–161, plate 34, Figs 69–70. ["Darjiling and Khasi Mts., India"]
- 1894 *Plectopylis plectostoma*, — Pilsbry: Manual of Conchology...: 2 (9): 146.
- 1897c *Plectopylis plectostoma*, — Gude: Science Gossip, 3: 274–275, Figs 39a–7c. ["Darjeeling", "Burma— Bassein and Arakan; Assam— Sylhet, Khasia and Naga Hills", "Dafla Hills in Assam"]
- 1899e *Plectopylis (Endothyra) plectostoma*, — Gude: Science Gossip, 6: 148, 149.
- 1899f *Plectopylis (Endothyra) plectostoma*, — Gude: Science Gossip, 6: 175, 177.
- 1914b *Plectopylis (Endothyra) plectostoma*, — Gude: The Fauna of British India...: 72, 73, 75, 81–83, Figs 31a–c. ["Naga Hills", "Dafla Hills, Khasi Hills", "Burma: Arakan Hills", "Tongoop", "Bassein: Pegu", "Sylhet", "Sikkim : Darjeeling"]
- 1922 *Plectopylis (Endothyra) plectostoma*, — Ehrmann: Sitzungsberichte der Naturforschender Gesellschaft zu Leipzig, 45–48: 8–10.
- 1959–1960 *Plectopylis (Endothyrella) plectostoma*, — Zilch: Handbuch der Paleozoologie, 6 (2): Fig. 2092.

Types: Darjeeling, coll MacAndrew excoll Benson, UMZC 102160 (7 syntypes); Darjeeling, coll MacAndrew excoll Benson, UMZC 102155 (1 syntype); Bengal, coll MacAndrew excoll Benson, UMZC 102156 (3 syntypes).

Material examined: Indien, Khasi Hills, ex Oberwimmer, NHMSB 122805–122810/5; Indien, leg. Stoliczka, coll. Oberwimmer, NHMW/4; Khasi Hills, leg. Stoliczka, 1870, NHMW 3; Viaggio in Birmania, Shweego, coll. Fea, 1885–1889, NHMW 20034/4; Khasi, coll. Stoliczka, 1880, NHMW/7; Khasi Hills, Himalaya, India, coll. Rušnov ex coll Blume, NHMW/3; Ostindien, Pegu, leg. Stoliczka, coll. Edlauer, 477, NHMW/8; Darjeeling, Himalaya, India, coll. Rušnov ex coll Blume, NHMW/5; Ostind., coll. Gerstenbrandt, NHMW 2745/2; Pegu, ex coll. Hauer, NHMW 21617/4; Asfam (?), coll Landauer, NHMW/2; Khasi Hills, Pegu (2 different label present in the sample), coll. Stoliczka, NHMW/41; Khasi, leg. Stoliczka, 1880, NHMW/7; Ost. Ind., coll. Gerstenbrandt, NHMW 2745/2; Khasi Hills, leg. Stoliczka, 1880, NHMW/approx. 70; Moulmein, Ceylon (erroneous locality), coll. Rušnov ex coll. Oberwimmer, NHMW/2; Brahmakund, O. Assam, India, coll. Rušnov ex coll. Blume, 1929, NHMW/1; India, Meghalaya, Khasi Hills, Altonaer Museum, ZMH 45909/4; East India, leg. Bernardi, Altonaer Museum, coll. O. Semper, ZMH 45908/1; Siam (erroneous locality), Altonaer Museum, ZMH 45910/2; S-Shan Staaten, Ywathit, Prov. Harenni, a. mittleren Salwen, leg. Michelitz, SMF 150108/3; Indien, Darjeeling, (alte Schau-sammlung), coll. Kobelt, SMF 150109/2; Indien, coll. Jetschin ex coll. Oberwimmer 1899, SMF 118089/2; Khasi Hills, coll. Bosch, ex coll. Rolle, SMF 172072/6; Darjeeling, Himalaya, coll. Jetschin ex coll. Oberwimmer 1899, SMF 118088/3; Birma, Moulmein, Hinterindien, coll. Krüper 1928, ex coll. Oberwimmer, SMF 118090/4; Khasi-Berge, coll. C. R. Boettger 1904, SMF 118091/1; Indien, Katschar, coll. Möllendorff, Orig. Handb. Pal. Fig. 2092; SMF 150106/4; Assam, coll. Dosch, ex coll. Rolle, SMF 172071/4; Indien, Khasi-Hills, coll. Webb 1928, SMF 150086/2; Darjiling, coll. Blanford, NHMUK 60.6.27.10/2; India, NHMUK/1; Teria Ghat, NHMUK 88.12.4.1536–1540/5; Pegu, coll. Godwin-Austen, NHMUK 1909.3.15.92/7; Naga Hills, coll. Godwin-Austen, NHMUK 1903.7.1.760/3; Pegu, Arakan, NHMUK 1903.7.1.758/3; Arakan, coll. Blanford, NHMUK 1909.3.15.60/3; Assam, Khasi Hills, coll. Salisbury ex coll. Beddome, NHMUK/3; Lhota Naga, coll. Chennell, NHMUK 1903.7.1.759/10; Sardia, E Assam, coll. Godwin-Austen, NHMUK 1903.7.1.761/8; Picholanulla, Durrang, Assam, coll. Godwin-Austen, NHMUK 1903.7.1.763/1; Khasi Hills, coll. Blanford, NHMUK 1906.2.2.356/4; Arakan, coll. Blanford, NHMUK 1906.2.2.355/4; India, NHMUK/5; Darjiling, NHMUK 1906.2.2.142/6; Shiroifurar, Lahupa Naga, coll. Godwin-Austen, NHMUK 1903.6.1.762/1; Darjeeling, 3500', leg. Lister, NHMUK 1907.9.13.11–22/11; India, NHMUK 71.9.23.206/3; no data, coll. Blanford, NHMUK/2; Manipur valley, Bisenfour (rest of the label not readable), NHMUK/25 (several of them are juvenile shells); N. Cachar, coll. Godwin-Austen, NHMUK/2; Teria Ghat, coll. Godwin-Austen, NHMUK/1; Cherra, Khasi Hills, Assam, coll. Godwin-Austen, NHMUK/25; Dunsiri valley, coll. Godwin-Austen, NHMUK/4; Khasi Hills, coll. Godwin-Austen, NHMUK/approx. 70; Garo Hills, NHMUK leg. W. Robert, coll. Godwin-Austen, NHMUK/27; Burma, Bassein, coll. Benson 1863, NHMUK/1; Khasi Hills,

NHMUK/3; Khasi Hills, NHMUK/3; Burreil Gorge, NHMUK/22; Manipur, NHMUK/ approx. 50; label not readable, NHMUK/7; Burreil, NHMUK/10; Khasi Hills, coll. Godwin-Austen, NHMUK/ approx. 80; Khasi Hills, coll. Blanford, NHMUK/3; W. Khasi Hills, coll. Godwin-Austen, NHMUK/1; N. Khasi, coll. Godwin-Austen, NHMUK/more than 100 shells; Pegu, NHMUK 92.9.3.15/7; Manipur, NHMUK/ many shells in 4 vials; Assam, coll. Steenberg, ZMUC-GAS-1812/2.

Differential diagnosis: See under *Endothyrella plectostoma exerta* and *E. plectostoma tricarinata*.

Characters of the genital structure: Two specimens have been anatomically examined. Collection data: Sikhim, leg. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.451. Both specimens had 5–6 embryos developing in their uterus.

The left ommatophoral retractor passes between penis and vagina. Atrium short; penis relatively short and of normal thickness, internally with holes of various sizes; some tiny, rounded calcareous crystal have been found in the penis lumen, not directly associated with the holes; this inner structure also continued in the epiphallus; penial caecum short, with a thickening in its middle; retractor muscle short, it inserts on the distal end of the penial caecum; epiphallus slightly longer than penis, it enters the distal penial portion laterally; vas deferens long and slender; vagina approximately as long as the penis, but thicker, it bents at its middle; vagina had several thick and relatively long muscle fibres attaching it to the body wall and to the diaphragm, especially at its curves portion; gametolytic sac and the additional organ next to it originate next to each other, the gametolytic sac is slightly thicker and shorter; a relatively long part of the spermooviductus was visible proximal to the thickened uterus having the developing embryos; the embryo sac contained no visible calcareous granules; albumen gland was conspicuously small.

Radula: Figure 7.107 and Table 7.4.

Distribution: Museum samples are labelled from several locations. The species is probably widely distributed in north-eastern India and also occurs very far from this region, namely in the Burmese Bago and the Arakan Hills (Figure 7.120).

Remarks: The name "*prodigium* Benson" probably refers to *Endothyrella plectostoma*. It is a manuscript name, which was mentioned several times in the literature (Godwin-Austen 1875, Tryon 1887, Pilsbry 1894, Gude 1899c), but has never been published formally.

***Endothyrella plectostoma exerta* (Gude 1901)**

Figure 7.24

1901c *Plectopylis plectostoma* var. *exerta* Gude: Journal of Malacology, 8: 49. Figs 5a–d.

1914b *Plectopylis (Endothyra) plectostoma* var. *exerta*, Gude, The Fauna of British India...: 83–84, Figs 33a–d. ["Assam: Khasi Hills"].

Types: Khasia Hills, ex Nissor (?), NHMUK 1922.8.29.50. (syntype).

Museum material examined: India, Khasia Hills; K4.30, coll Rolle, NHMW 50854/2; Assam, Khasia Hills, coll. Dosch, ex coll. Rolle, SMF 172073/3; Assam, Cherrapunjee, coll. Jetschin, ex coll. Gude 1900, (labelled as syntype, but it is not), SMF 118097/1; Assam, coll. Ehrmann ex coll. Schlüter, SMF 150113/1; Khasi Hills, coll. Blanford, NHMUK 1906.1.1.743/2; Khasi Hills, India, Assam (!), NHMUK 1916.3.16.6–7/2; Khasi Hills, coll. Kennard, NHMUK/4; Khasi Hills, Assam, NHMUK/3; Khasi Hills, Bengal, NHMUK/2; Khasi Hills, India, NHMUK/2;

Differential diagnosis: According to the original description, *E. plectostoma exerta* "differs from the type in the peripheral keel being exerted" (= whorls are shouldered above). "The shell is also larger and more solid".

Distribution: The subspecies is known from the type locality only.

***Endothyrella plectostoma tricarinata* (Gude 1896)**

Figure 7.24

1897c *Plectopylis plectostoma* var. *tricarinata*, — Gude: Science Gossip, 3: 275, Figs 40a–b. ["Bengal"]

1897l *Plectopylis plectostoma* var. *tricarinata*, — Gude, The Journal of Malacology, 6: 45–46, Fig. 2. ["Bengal"]

1899e *Plectopylis (Endothyra) plectostoma* var. *tricarinata*, — Gude: Science Gossip, 6: 148.

1899f *Plectopylis (Endothyra) plectostoma* var. *tricarinata*, — Gude, Science Gossip, 6: 176, 177.

1914b *Plectopylis (Endothyra) plectostoma* var. *tricarinata*, — Gude: The Fauna of British India...: 83, Figs 32a–b. ["Bengal", "Khasi Hills"]

Types: Bengal, coll MacAndrew ex coll Benson, UMZC 102170 (2 syntypes).

Differential diagnosis: According to the original description, *Endothyrella plectostoma tricarinata* "differs from the type in being larger, in having the periphery acutely keeled, and in having three raised ridges between the periphery and the suture, revolving as far as the fourth whorl".

Distribution: The subspecies is known from the type locality only.

***Endothyrella nomenovum*1 Páll-Gergely nom. nov. pro *Helix (Plectopylis) minor* Godwin-Austen 1879**
Figure 7.22

1870 *Helix (Plectopylis) minor* Blanford, Journal of the Asiatic Society of Bengal, 39 (2): 18. ["in valle Rungnu prope Darjiling in Sikkim"]

1879b *Helix (Plectopylis) minor*, — Godwin-Austen: The Annals and Magazine of Natural History, 5 (4): 164. ["Darjiling hills"]

1895 *Helix (Plectopylis) minor*, — Godwin-Austen, — Journal of the Asiatic Society of Bengal, 64: 154, plate 7, Figs 3, 3a.

1897f *Plectopylis minor*, — Gude: Science Gossip, 4: 11, Figs 47 a–k. ["Darjeeling"]

1899e *Plectopylis (Endothyra) minor*, — Gude: Science Gossip, 6: 148.

1899f *Plectopylis (Endothyra) minor*, — Gude: Science Gossip, 6: 175, 177.

1914b *Plectopylis (Endothyra) minor*, — Gude: The Fauna of British India... 73, 75–77, Figs 27a–l. ["Sikkim: Darjeeling", "Rungun Valley", "India: Naga Hills", "Laisen Peak, Munipur"].

Types: See under remarks.

Museum material examined: Nepal, Lalitpur, Phulchowki Hill, 2308 m, 27.574557°N, 85.400842°E, leg. Budha, P., 04.05.2007., 21 shells; Nepal, Kathmandu, Chisapani, Shivapuri-Nagarjun National Park, 2361 m, 27.804855°N, 85.436468°E, leg. Budha, P., 11.06.2007., 5 shells; Nepal, Golphubhanjyan, Langtang National Park, Rasuwa, 3340 m, 27.873931°N, 85.757744°E, leg. Budha, P., 10.06.2007., 1 shell; Nepal, Shivapuri-Nagarjun National Park, Deurali, Baghdwar, 2386 m, 27.798318°N, 85.385448°E, leg. Budha, P., 25.04.2008., 1 shell; Nepal, Shivapuri-Nagarjun National Park, Shivapuri Peak, 2707 m, 27.810987°N, 85.383763°E, leg. Budha, P., 24.04.2008., 1 shell; India, Darjiling, leg. Stoliczka, coll. Oberwimmer, NHMW 6881/4; Darjeeling, coll. Rolle, NHMW/3; Darjiling, coll. Dr. Stoliczka, 1880, NHMW/20; Darjeeling, coll. Webb, SMF 150111/2; Sikkim, coll. Godwin-Austen, NHMUK (mixed sample with *E. blanda*); Khasi Hills, NHMUK/2; Sikkim, Rarhichu, NHMUK (mixed sample with *E. blanda*); India, Darjeeling, coll. Oldham, NHMUK/5; India, 79.12.26.172–177/5; Sikkim, NHMUK 1906.2.2.361/3; Darjeeling, NHMUK/1; Sikkim, NHMUK 88.12.4.1525(?)1; Darjeeling, under stones, 7000', coll. Everest Expedition 9 and 18.03.1924, NHMUK/5; Khasi Berge, SMF 345110/3 (ex *E. macromphalus*, SMF 150102).

Diagnosis: A minute (ca. 4–5 mm), sinistral species with relatively narrow umbilicus, flat dorsal surface and four rows of hairs. Callus strong; palatal plicae divided; lamella straight or slightly curved, with two denticles posteriorly, one above and one below.

Differential diagnosis: *E. macromphalus* is hairless and larger, has comparatively larger protoconch and lower (or missing) parietal callus. See also under *E. species4* u. sp., *E. blanda*, *E. species5* u. sp. and *E. williamsoni*.

Measurements (in mm): D= 4–5, H= 2–2.5, Wh= 5–5.5 (n=12, Nepalese specimens)

Distribution: Originally the species was recorded from Darjeeling, Sikkim area. Very similar specimens were found in from Central Nepal in the surroundings of Kathmandu (Langtang National Park, Shivapuri-Nagarjun National Park and Phulchowki hill). Some literature records (Laisen Peak, Naga Hills) are based on misidentified specimens (Figure 7.121 and Figure 7.123).

Remarks: Blanford (1870) described *Helix (Plectopylis) macromphalus*, and while giving information on its locality, he mentioned that "varietas minor" inhabits the Rungnu valley near Darjeeling. No description or illustration of "varietas minor" have appeared in the same paper, therefore the name is not available. Later, Godwin-Austen (1879b) described *Helix (Plectopylis) minor* from "Darjiling hills" and mentioned those shell "no doubt are referable to *P. macromphalus* W. Blf., var. *minor*". Blanford's specimens having labelled as *macromphalus minor* have not been found in the collection of the NHMUK. Also, Type material of *Helix (Plectopylis) minor* were not present in the type collection of the NHMUK. One sample, "*Plectopylis minor*, Darjiling, coll. Hungerford ex Nevill, NHMUK 1891.3.17.358–9." contains two shells which are "probably syntypes", because in the original description Godwin-Austen mentioned that he received shells from Nevill from Darjiling. The only reason I am hesitant to say "syntypes" is the name of Hungerford on the label which is not mentioned in the description and the handwriting on the labels is not Godwin-Austen's.

Godwin-Austen's (1879b) *Helix (Plectopylis) minor* is a junior synonym of *Helix nemoralis* var. *minor* Charpentier, 1837, which is the oldest valid trinomial use of the name *minor* within *Helix* (Neubert 2014). Therefore, a new name must be added for this species. I suggest the name *Endothyrella nomenovum*1 as nomen novum for the taxon.

Recent field investigations in Nepal resulted in the discovery of a few populations in the surroundings of Kathmandu which can be assigned to *E. nomenovum*1. "Typical" specimens of *E. nomenovum*1 and Nepalese shells are very similar in terms of size, shell and aperture shape and the morphology of the plicae and lamellae. The only notable difference between these shells is the position of the hair rows on the body whorl. The first row is situated more upper in position (on the upper angle of the body whorl) in the Nepalese shells, whereas in typical shells the first row runs under the angle. Additionally, the distance between the third and fourth rows is smaller in the Nepalese populations.

Endothyrella serica (Godwin-Austen, 1875)

Figures 7.23, 7.30, 7.41

- 1875b *Helix (Plectopylis) serica* Godwin-Austen: Proceedings of the Zoological Society of London: 608, 609, 612, plate 73, Figs 5, 5a–c. ["I first collected this shell on the peak of Henozdan, Burrail range, in the spring of 1868. I again found it abundant above 5000 feet on the same range as far east as the Kopamedza ridge. It is essentially a forest species, found in the dead leaves and moss at the foot of the trees"]
- 1875b *Helix (Plectopylis) munipurensis* Godwin-Austen: Proceedings of the Zoological Society of London: 610, 612, plate 73, Figs 6, 6a–c. ["At the end of the Ihang valley, Munipur, at about 3000-4000 feet"]
- 1875 *Helix sericata* (sic!), — Hanley & Theobald: Conchologia Indica...: 53, plate 132, Figs 8, 9.
- 1878a *Helix (Plectopylis) serica*, — Nevill: Hand list of Mollusca in the Indian Museum, Calcutta...: 71. ["Hengdan Peak and Burrail"]
- 1879a *Helix (Plectopylis) serica*, — Godwin-Austen: Journal of the Asiatic Society of Bengal, 48 (2): 3. ["Burrail Range"]
- 1887 *Helix (Plectopylis) serica*, — Tryon: Manual of Conchology..., 2 (3): 159, plate 34, Figs 49–52. ["Burrail Mts, India"]
- 1887 *Helix (Plectopylis) Munipurensis*, — Tryon: Manual of Conchology..., 2 (3): 160, plate 34, Figs 56–58. ["Munipur, India; alt. 3000-4000 ft"]
- 1897a *Plectopylis serica*, — Gude: Science Gossip, 3: 205–206, Figs 31a–c. ["peak of Henozdan, Burrail Range, Naga Hills"; "above 5,000 feet on the same range as far east as the Kopamedza ridge"; "Sylhet"]
- 1897b *Plectopylis serica*, — Gude: Science Gossip, 3: 246. ["Hengdan" and "Kopamedza"]
- 1898b *Plectopylis munipurensis*, — Gude: Science Gossip, 4: 263–264, Figs 69a–g.
- 1899e *Plectopylis (Chersaecia) serica*, — Gude: Science Gossip, 6: 148.
- 1899e *Plectopylis (Chersaecia) munipurensis*, — Gude: Science Gossip, 6: 148.
- 1899f *Plectopylis (Chersaecia) serica*, — Gude: Science Gossip, 6: 175, 177.
- 1899f *Plectopylis (Chersaecia) munipurensis*, — Gude: Science Gossip, 6: 175, 176.
- 1914b *Plectopylis (Chersaecia) serica*, — Gude: The Fauna of British India...: 73, 93–94, Figs 40a–c. ["Hengdan and Kopamedza Ridge, 5,000 ft, Burrail Range, Naga Hills" and "North Cachar"]
- 1914b *Plectopylis (Chersaecia) munipurensis*, — Gude: The Fauna of British India...: 73, 94–95, Figs 41a–g. ["Burma: Ihang Valley, Munipur"]

Types: Khunho, H.S. Naga Hills, leg. Godwin-Austen, NHMUK 1903.7.1.741 (8 syntypes of *serica*); Hengdan P., Naga Hills, leg. Godwin-Austen, NHMUK 1903.7.1.744 (6 syntypes of *serica*); Munipur Hills, head of the Ihang valley, Munipur, leg. Godwin-Austen, NHMUK 1903.7.1.742. (6 syntypes of *munipurensis*).

Museum material examined: Naga Hills, coll. Godwin-Austen, NHMUK 1903.7.1.743/4; Japvo Peak, Nr. Kohima, Naga Hills, NHMUK/8; Lhota Naga, coll. Godwin-Austen, NHMUK 1903.7.1.745/6; no locality, leg. Maxwell, coll. Godwin-Austen, NHMUK/5; India, Hengdan Peak, NHMUK 91.3.17.356–357/2; India, NHMUK 74.4.26.2/3; Khasi Hills, coll. Blandford, NHMUK 1906.2.2.360/2;

Diagnosis: A small (10.5–11 mm), dextral, yellowish-reddish striped species with moderately wide umbilicus and depressed conical dorsal surface. Callus strong, palatal plicae more or less straight, simple or have dichotomously divided posterior ends; parietal wall with a single curved lamella with denticles near the upper and lower ends posteriorly, which occasionally fuse to the lamella.

Differential diagnosis: See also under *E. babbagei*, *E. species6* u. sp. and *E. oglei*, and under the remarks.

Distribution: The species is recorded from the Naga Hills (see also remarks). "*Plectopylis manipurensis*" was described from "end of the Ihang valley". The Ihang River is probably a minor river in Manipur (Figure 7.123).

Remarks: Godwin-Austen described *Helix (Plectopylis) serica* and *Helix (Plectopylis) manipurensis* in the same publication. He has not mentioned the differences between the two species. According to the illustrations, the upper end of the lamella in *manipurensis* is more elongated anteriorly than that of *H. serica*. A *serica* shell from Hengdan sample, however, has equally long upper plica, similar to *manipurensis* shells. Examining the type material of the same species I have not found any additional considerable differences. Therefore I synonymize *manipurensis* with *serica*. *Helix (Plectopylis) serica* had the priority since it was introduced earlier in the same publication.

In the original description Godwin-Austen (1875) reported the species from the "peak of Henozdan" and from the "Kopamedza ridge". The second sample is probably identical with the one from Khunho in the type collection of the NHMUK.

Gude (1897h) mentions that according to Godwin-Austen, the names "Henozdan" and "Kopameda" in Gude (1897) are correctly "Hengdan" and "Kopamedza", respectively. According to the same erratum, Godwin-Austen also mentioned that the locality of Ponsonby's shell (Sylhet) is probably incorrect, because *Plectopylis serica* is a very local species, inhabiting higher altitudes than 5.000 feet.

***Endothyrella sowerbyi* (Gude 1898)**

Figure 7.24

1899a *Plectopylis sowerbyi* Gude: Science Gossip, 5: 239, Figs 93a–f. ["Khasi Hills: Assam"]

1899e *Plectopylis (Endothyra) sowerbyi*, — Gude: Science Gossip, 6: 148, 149.

1899f *Plectopylis (Endothyra) sowerbyi*, — Gude: Science Gossip, 6: 175, 177.

1914b *Plectopylis (Endothyra) sowerbyi*, — Gude: The Fauna of British India...: 72, 80–81, Figs 30a–f. ["Assam: Khasi Hills"]

1915 *Plectopylis (Endothyra) sowerbyi*, — Gude: Records of the Indian Museum, 8: 507, 509.

Types: Khasia Hills, India, NHMUK 1922.8.29.48. (holotype)

Differential diagnosis: The most similar species is *Endothyrella plectostoma*. The differences between *E. sowerbyi* and *E. plectostoma* are the following: palatal plicae are divided in *plectostoma* but not divided in *sowerbyi*, *E. sowerbyi* is flatter and has wider umbilicus, and it lacks the main plica which is present in *E. plectostoma*. Moreover, the peristome of *E. sowerbyi* is thinner and less reflexed than that of *E. plectostoma*, and the callus of *E. sowerbyi* is missing.

Distribution: The species is known from the type locality only (Figure 7.123).

Remarks: *Endothyrella sowerbyi* may be conspecific with *E. plectostoma*. More material would be necessary to verify that hypothesis.

***Endothyrella williamsoni* (Gude 1915)**

Figures 7.27, 7.41

1915 *Plectopylis (Endothyra) williamsoni* Gude: Records of the Indian Museum, 8: 509, plate 42, Figs 1a–d. ["Abor Hills, exact part not indicated"]

Types: Abor Hills, leg. C.F.G. Oakes, R.E., NHMUK 1903.7.1.3087.

Diagnosis: A very small (6 mm), probably hairless, sinistral species with narrow umbilicus and conical dorsal surface. Callus strong, palatal plicae horizontal, almost straight and thin at their middle. Lamella slightly curved; there is long, horizontal plica anteriorly to the lamella, and a short horizontal plica above the long one. Additionally, there is a very short upper plica above the lamella, a small denticle posteriorly above, and a long lower plica near the suture which reaches the aperture.

Differential diagnosis: Has more elevated spire than *E. macromphalus* and *E. nomenovum*1. The most similar species in terms of shell shape is *E. blanda*. For comparisons, see under that species.

Distribution: The species is known from the type locality only (Figure 7.122).

Genus *Gudeodiscus* Páll-Gergely 2013

Type species: *Plectopylis phlyaria* (Mabille 1887a) by original designation.

Content: *Gudeodiscus* (*Gudeodiscus*) and *Gudeodiscus* (*Veludiscus*).

Diagnosis: Shell rarely small, usually middle sized or large, dextral, body whorl rounded, there are no periostracal folds on the "upper keel" of the whorls. The whole protoconch is usually very finely, regularly ribbed (see Figure 7.30–7.31). Only known exceptions are *G. villedaryi* (see Figure 7.31E) 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 "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 (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: *Sinicola* species have keeled body whorl, most of them have periostracal folds standing in a single row on the keel and the inner wall of their penis lacks characteristic pockets. "Western" *Sicradiscus* species (*invius*, *feheri*, *mansuyi*, *securus*) have small shells with glossy bases and strong apertural folds. This combination of characters does not occur in *Gudeodiscus*. Eastern *Sicradiscus* species (*diptychia*, *transitus*, *ishizakii*, *hirasei*, *schistoptychia*) have keeled/shouldered body whorl occasionally with periostracal folds. Moreover, as far as known, their penises lack the pockets which are characteristic for *Gudeodiscus*. *Halongella* species lack the penial caecum (usually present in *Gudeodiscus*), and has only parallel rows on the inner wall of the penis (*Gudeodiscus* has characteristic pockets). Additionally, the longitudinal folds on the inner wall of the epiphallus of *Halongella* species have transversal projections which overlap with those of the neighbouring folds. *Gudeodiscus*, however, has only parallel folds inside the epiphallus. Moreover, most anatomically examined *Gudeodiscus* specimens had a penial caecum, which is missing in both *Halongella* species. Genus3 is characterized a protoconch which is densely ribbed, and the ribs are wavy, whereas the ribs are straight in *Gudeodiscus*. Moreover, Genus3 lacks the epiphallus, which is well developed in all *Gudeodiscus* species which are known anatomically.

Distribution: Northern Vietnam, Southern China (Guangxi, Hong Kong, Southern Hunan) (Figure 7.127).

Subgenus *Gudeodiscus* Páll-Gergely, 2013

2015 *Gudeodiscus* (*Gudeodiscus*) Páll-Gergely et al., Zookeys 472: 13.

Content: *anceyi* (Gude 1901)?, *concaus* Páll-Gergely 2013?, *cyrtochilus* (Gude 1909)?, *dautzenbergi* (Gude 1901), *fischeri* (Gude 1901), *francoisi* (H. Fischer 1899)?, *giardi* (H. Fischer 1898), *hemmeni* Páll-Gergely & Hunyadi u. sp.?, *infralevis* (Gude 1908)?, *marmoreus* Páll-Gergely 2014?, *messengeri* (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?.

Diagnosis: Shell indistinguishable from *Gudeodiscus* (*Veludiscus*) and *Halongella*. 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.

Differential diagnosis: See under *Gudeodiscus* (*Veludiscus*).

Remarks: All known *Gudeodiscus* species are classified 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 the subgeneric status is questionable. These are indicated by a question mark after the name of the subgenus. The shell and *G. dautzenbergi* is very similar to the nearby occurring *G. villedaryi*, therefore I think there is no need to question the subgeneric status.

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

Figures 7.15, 7.42

- 1901b *Plectopylis Anceyi* Gude, Journal de Conchyliologie, 49: 208–209., Figs 6 a–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.
2015 *Gudeodiscus (Gudeodiscus?) anceyi*, — Páll-Gergely et al., Zookeys 472: 14, Figs 2B, 9G, 11C–F.

Types examined: Tonkin, Bac-Kan, leg. Messenger, MNHN 24600 (syntype); 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 Messenger, SMF 150135/1; Central-Tonkin, Chiam-Hoa, coll. Möllendorff ex Fruhstorfer SMF 150134/1; Tonkin, Bac-Kan, leg. Messenger, 22.11.1898, RBINS/5; Secteur de Nac-Ri, RBINS/1; Secteur de Nac-Ri, leg. Messenger (n. 33), RBINS/1; Tonkin, entre Cho-Moi, et That-Khé, leg. Messenger (n. 33), RBINS/11; Tonkin, Bac-Kan, RBINS/4; Muong-Kong, leg. Messenger, MNHN-IM-2012-2139/1; Secteur de Nac-Ri, Bac-Kan, leg. Messenger, MNHN-IM-2012-2250/343; Bac-Kan, leg. Messenger, MNHN-IM-2012-2252/60; Bac-Kan, leg. Messenger, MNHN-IM-2012-2258/38; That-Khé, coll. Mansuy, MNHN-IM-2012-2259/12; Cho-Moi, leg. Messenger, MNHN-IM-2012-2263/48; Bac-Kan, leg. Messenger, MNHN-IM-2012-2265/30; Long-Phai, leg. Messenger, MNHN-IM-2012-2270/36; Cho-Moi, leg. Messenger, MNHN-IM-2012-2275/30; Long-Phai, leg. Messenger, MNHN-IM-2012-2277/26; Cho-Moi, leg. Messenger, MNHN-IM-2012-2283/95; Cao-Bang, leg. Messenger, MNHN-IM-2012-2468/1; Na-Ri, leg. Messenger, MNHN-IM-2012-2285/40; Long-Phai, leg. Messenger, MNHN-IM-2012-2286/36; Bac-Kan, coll. Letellier, 1949, MNHN-IM-2012-2287/1; Cho-Moi, leg. Messenger, MNHN-IM-2012-2300/25; Bac-Kan, coll. Lavezzari, 1929, MNHN-IM-2012-2301/15; Bac-Kan, leg. Messenger, MNHN-IM-2012-2305/62; Long-Phai, leg. Messenger, MNHN-IM-2012-2312/30; Bac-Kan, coll. Staadt, 1969, MNHN-IM-2012-2313/4; Na-Ri, leg. Messenger, MNHN-IM-2012-2376/34; Pakhé, leg. Messenger, 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 Messenger, NHMW 92556/6; Tonkin, Bac-Kan, coll. Wagner ex Messenger, NHMW 92557/2; Tonkin, Cho-Moi, coll. Oberwimmer ex Rosen, NHMW 71640/O/9480/1; Tonkin, Ngam-Son, coll. Wagner ex Messenger, NHMW 82558/2; Tonkin, Cho-Moi, coll. Rosen, NHMW 71640/O/9479/2; Tonkin, Bac-Khan, coll. Rolle ex Messenger, 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 Phong cave, GPS not recorded, leg. Hemmen, Ch. & J., 10.10.2010., PGB/1; **GS21** Bắc Kạn Prov, Na Ri Distr., 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°16'51.63"N, 106°02'10.11"E, leg. Grego, J. & Šteffek, J., 06.04.2012.; **GS22** Bắc Kạn Prov, Na Ri Distr., 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, 587 m, 22°14'32.81"N, 106°00'31.65"E, leg. Grego, J. & Šteffek, J., 06.04.2012., PGB/1; **GS24** Bắc Kạn Prov, Na Ri Distr., 2 km S of Bản Dền, W slopes of a deep sinkhole covered with forest, leaf litter under high limestone wall, 637 m, 22°14'30.36"N, 106°00'31.27"E, leg. Grego, J. & Šteffek, J., 06.04.2012.; **2011/82** Lạng Sơn Province, Lũng Phây Pass, Thát 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 National 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 National Park, Thảm Kịt Cave 2 km, look-out 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, Bồ 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 Phong Cave, south of Bồ 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 Ri 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 Prov., 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, Đông Đăng to Thái Nguyên (8 km S Bắc Sơn), 21°54.543'N, 106°17.298'E, leg. Hemmen, Ch., 02.04.2011., HE/7; **Vn11-31C** Bắc Kạn Province, Ba Bể N. P., near Puông Cave, 22°27.835'N, 105°38.997'E, leg. Hemmen, Ch., 17.03.2011., HE/1; same data, leg. Hemmen, Ch., 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. 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.

Differential diagnosis: *G. messengeri* is larger than *G. anceyi*, lacks the apertural fold and spiral lines on the ventral surface of the shell. *G. 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 and flatter than *G. anceyi*, they often lack the apertural fold. For differences with *G. hemmeni* u. sp. and *Sicradiscus mansuyi*, see descriptions under those species.

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).

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: I have seen newly-collected material only from Bắc Kạn Province. The species was previously recorded from That Khê (Lạng Sơn Province) and Nac Ri (Hà Giang Province) (Gude 1901b) (Figure 7.115).

***Gudeodiscus (Gudeodiscus?) concavus* Páll-Gergely 2013**

Figures 7.11, 7.44

2013 *Gudeodiscus concavus* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 11, Figs 19, 51a–b.

2015 *Gudeodiscus (Gudeodiscus?) concavus*, — Páll-Gergely et al., Zookeys 472: 13.

Type material: Guangxi, Huanjiangmaonanzu Zizhixian, Shuiyuan Zhen, Guangnan, 238 m, 24°49.217'N, 108°06.386'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 19.10.2011, holotype HNHM 97440, paraType material: HA/1, OK/3, PGB/2.

Diagnosis: A medium-sized, flat species with concave dorsal surface. There is a short apertural fold and a single lamella on the parietal wall with two short plicae anteriorly.

Description: Shell brownish-corneous, flat; dorsal surface concave; whorls 6.25–6.5, separated by rather deep suture; teleoconch finely, irregularly reticulated; umbilicus very wide; aperture oblique, with thickened and slightly reflected lip; callus slightly S-shaped, with canals at both ends; apertural fold short, free from the callus.

Three specimens were opened. Parietal wall with a single oblique lamella and very weak horizontal plicae above and below; palatal side with seven very short plicae, first and last straight, the others have depressed Z-shape.

Differential diagnosis: The concave dorsal surface and the extremely oblique aperture are very characteristic for this species. Additionally, it has lighter shell, rougher sculpture, stronger fold and callus than *G. eroessi fuscus*. *G. concavus* is much smaller with thinner shell wall and wider umbilicus than *G. pulvinaris robustus*.

Measurements (in mm): D= 18.1–20.4, H= 6.2–6.9 (n=3).

Etymology: The name of this species refers to the concave dorsal surface of the shell.

Type locality: Guangxi, Huanjiangmaonanzu Zizhixian, Shuiyuan Zhen, Guangnan, 238 m, 24°49.217'N, 108°06.386'E.

Distribution: This species is known from the type locality only (Figure 7.113).

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

Figures 7.10, 7.46, 7.47

1909 *Plectopylis cyrtochila* Gude, Proceedings of the Malacological Society of London, 8 (4): 217, pl. 9, Figs 5, 5a–b.

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

2015 *Gudeodiscus* (*Gudeodiscus*?) *cyrtochilus*, — Páll-Gergely et al., Zookeys 472: 17, Figs 2F, 15E–G.

Types examined: Tonkin, Moung-Kong, leg. Messenger, NHMUK 1922.8.29.59 (syntype).

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

New material examined:

Vietnam: **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, 1088 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., 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., 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., 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., 23.03.2011., HE/3. **China:** Yunnan, about 36 km S of Guangnan, northern end of Kongshan Cun, 1556 m, 23°42.950'N, 105°04.570'E, leg. Hunyadi, A., 23.3.2011, HNHM 97445, NHMUK 20120005/1; NHMW 108172/1, SMF 341506/1, HA/26 + 6 damaged, PGB/3; Western Yunnan, about 20 km NW of Funing Xian, Sanla waterfalls, 1010 m, 23°45.350'N, 105°30.067'E, leg. Hunyadi, A., 24.3.2011, HA/17 + 4 damaged shells.

Diagnosis: Shell very small to small, discoid, polished shell 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 plicae; 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.

Description: Shell discoid, thin-walled, glossy, yellowish corneous; dorsal side with fine, irregular growth lines; weaker growth lines on ventral side; whorls 5.75–6.5, separated by relatively shallow suture; aperture with very weak callus and white, thin and slightly reflected apertural lip; no fold in the aperture; umbilicus moderately wide but deep.

Two Chinese specimens were opened. Parietal wall with two well-developed lamellae; first stronger, supported by two plicae above and below; in one of the opened specimens both the upper and lower plicae were free, but in the other one the anterior lamella was in contact with both plicae; five or six plicae on the palatal wall; first plicae close to the suture, vestigial, in some cases totally missing; other plicae (second–fifth) are of the same length, straight and connected with a continuous ridge.

Differential diagnosis: The Chinese *Gudeodiscus yunnanensis* Páll-Gergely & Hunyadi 2013 has a similar shell shape but possesses only one vertical parietal lamella. The two species can be separated only the basis of the presence or absence of the anterior lamella. In *G. soosi* Páll-Gergely 2013 and in most specimens of *G. multispira* (Möllendorff 1883), 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*. *G. infralevis* is larger with a more elevated spire, stronger apertural lip and usually a weak apertural fold. See also under *G. fisheri*.

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 & Hunyadi 2013).

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: The species was described from "Muong-Kong" (=Mường Khương, Lào Cai Province). I have noted material from northeast of this locality, from northern Hà Giang Province and eastern parts of Yunnan Province (China) (see Páll-Gergely & Hunyadi, 2013) (Figure 7.116).

Remarks: The drawing in the original description of *G. 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 *Endothyrella* (*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 7.5, 7.6, 7.45

1901b *Plectopylis Dautzenbergi* Gude, Journal de Conchyliologie, 49: 198–200., Figs 1a–f. Plate 6, Figs 1a–c. ["That Khé (le type); entre Cho-Moi et Bac-Kan; entre Bac-Kan et Nac-Ri"]

1901b *Plectopylis persimilis* **new synonym** Gude, 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.

2015 *Gudeodiscus (Gudeodiscus) dautzenbergi*, — Páll-Gergely et al., Zookeys 472: 19, Figs 8E–F, 9K–L, 14A–G.

Types examined: Tonkin, That-Khé, MNHN 24603 (holotype of *dautzenbergi*), Environs de That-Khé, leg. Messenger (n. 22.), MNHN 24602 (holotype of *persimilis*).

Museum material examined: Tonkin, Nja-Ba-Thà, coll. Dosch ex Rolle, SMF 341738/1; Tonkin, That-Khé, coll. Dorsch ex Rolle ex Messenger, SMF 172083/2; Tonkin, coll. Jetschin ex Bonnet 1900, SMF 102823/1; Fr. Indochina, Tonkin, That Ké, leg. Demange, 1911, HNHN 10278/2; Tonkin, coll. Sayer 1969, MNHN-IM-2012-2273/1; Tonkin, coll. Letellier 1949, MNHN-IM-2012-2274/1; Bac-Kan, leg. Messenger 1904, coll. Lavezzari, 1929, MNHN-IM-2012-2290/5; Tonkin, leg. Messenger, MNHN-IM-2012-2292/2; Bac-Kan, leg. Messenger, MNHN-IM-2012-2297/2; Tonkin, coll. Denis 1946, MNHN-IM-2012-2303/4; Bac-Kan, leg. Messenger, MNHN-IM-2012-2314/7; That Khé, leg. Messenger, MNHN-IM-2012-2327/4; Bac-Kan, leg. Messenger, MNHN-IM-2012-2331/5; Bac-Kan, leg. Messenger, MNHN-IM-2012-2437/1; Bac-Kan et That Khé, coll. Staadt 1969, MNHN-IM-2012-2280/2; Na-Ri, leg. Messenger, MNHN-IM-2012-2461/1; That-Khé, leg. Messenger, MNHN-IM-2012-2373/6; That-Khé, leg. Messenger, MNHN-IM-2012-2378/4; Bac-Kan, leg. Messenger, MNHN-IM-2012-2382/4; Bac-Kan, leg. Messenger, MNHN-IM-2012-2383/4+14 juvenile shells; Bac-Kan, leg. Messenger, MNHN-IM-2012-2402/3; Than-Moi, coll. Staadt, 1969, MNHN-IM-2012-2336/1; Bac-Kan, leg. Messenger, MNHN-IM-2012-2337/26+2 juvenile shells; That-Khé, leg. Messenger, MNHN-IM-2012-2354/4; Cao-Bang, leg. Messenger, 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 Messenger, NHMW 71640/O/10285/1 (mixed sample with *schlumbergeri*); Bac Kan, coll. Steenberg, ZMUC-GAS-1084/1.

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 reaches its maximum height some distance from the callus. 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.

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 similarly looking populations of *Gudeodiscus 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*). *G. 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 *Halongella schlumbergeri* requires experience, but is possible without breaking the shell on the basis of the formation of the peristome and the apertural fold.

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).

Intraspecific diversity: Low; shell characters stable.

Distribution: This species as well as *Plectopylis persimilis* (synonym of *G. dautzenbergi*) were described from That-Khé (northern Lạng Sơn Province). My newly-collected material is from the border region of the Thái Nguyên and Bắc Kạn provinces (Figure 7.115).

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 I synonymise *Plectopylis persimilis* with *P. dautzenbergi*. These two species were described in the same publication (Gude 1901b), therefore the name introduced earlier (*dautzenbergi*, page 198) is considered valid.

Here I separate *G. dautzenbergi* and *G. villedaryi* 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* from *G. villedaryi*.

The specimen figured by Zilch (1960, Fig. 2094) under the name *Plectopylis (Endoplion) 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 7.9, 7.46, 7.60, 7.61, 7.91, 7.94–7.96, 7.100

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

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

1905b *Plectopylis Fischeri*, — Dautzenberg & Fischer, Journal de Conchyliologie, 53 (4): 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.

2015 *Gudeodiscus (Gudeodiscus) fischeri*, — Páll-Gergely et al., Zookeys 472: 21, Figs 2E, 3A–C, 9P–Q, 15H–R, 17, 18, 28D, 29D, 29J, 30E, 31D, 34M–O.

Types examined: Tonkin, Environs de Bac-Kan, leg. Messenger, MNHN 24579 (holotype of *fischeri*); Tonkin, Cho-Ra, leg. Messenger, MNHN 24587 (holotype of *tenuis*).

Museum material examined: Tonkin, Bac-Kan, NHMUK 1908.12.21.144/1; Tonkin, environs de Bac-Kan, leg. Messenger, (n. 28), RBINS/2; Tonkin, Ha-Giang, leg. Messenger, RBINS/5; Ha Giang, leg. Mansuy, coll. M. H. Fischer, MNHN-IM-2012-2241/12 adult, 1 juvenile shell; Ha Giang, coll. Mansuy, MNHN-IM-2012-2257/5; Tonkin, leg. Messenger, MNHN-IM-2012-2390/1; Cho-Ra, leg. Messenger, MNHN-IM-2012-2477/1; Bac-Kan, leg. Messenger, MNHN-IM-2012-2466/3; Tonkin, Cho Ra, ex Rolle, USNM 207813/2 ("*tenuis*"); Nga-Son, leg. Messenger, MNHN-IM-2012-2233/2 ("*tenuis*"); Nga-Son, leg. Messenger, MNHN-IM-2012-2253/2 ("*tenuis*"); Tonkin, coll. Denis, 1946, MNHN-IM-2012-2338/3 ("*tenuis*"); Cho-Ra, leg. Messenger, 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, 73 m, 22°08.673'N, 104°58.634'E, leg. Ohara, K., 19.05.2009., OK/12, PGB/3; **20090515C** Bắc Kạn Province, Ba Bê District, Ba Bê Nat. Park, Khâu Kùm, 184 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), 113 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 Hồng, 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); **Vn10-120** Hà Giang Province, ca. 9.8 km from Hà

Giang to Tam Son (formerly Quận 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 Son, 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 Son, 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*"); **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, Thăm 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 (anatomically examined) ("*tenuis*"); **2011/97** Bắc Kạn Province, Ba Bể Nat. Park, Thăm 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 shiny); 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. Parietal wall with two lamellae (the anterior is exceptionally dissolved); middle palatal plicae oblique, depressed Z or L-shaped, they are free or sometimes connected to each other.

Differential diagnosis: *Gudeodiscus cyrtochilus* is smaller, has a narrower umbilicus, more regularly growing whorls (the last whorl is only slightly wider than the penultimate one), shorter lower horizontal parietal plicae 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. In some populations of *G. multispira* the denticles are missing so that only the posterior lamella is present. *G. yunnanensis* has no anterior lamella, just a curved single lamella (homologous with the posterior lamella). *G. eroessi* never has apertural fold and its anterior lamella is dissolved or missing. *G. infralevis* and *G. suprafilaris* have more elevated spire, narrower umbilicus and rather straight, horizontal, parallel plicae.

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, 2009.05.19B), D= 15.5–15.9, H= 7.1–7.2. (n=2, 2009.05.15C), 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).

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.

Characters of the genital structure: Two specimens were dissected, belonging to two different populations: "Specimen1" Tuyên Quang Province, near Tôn Hồng, 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); "Specimen2" Bắc Kạn Province, Ba Bể Nat. Park, Thăm 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).

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 strongly 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 about 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, longitudinal, serrulate folds; 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; spermoviduct 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: Figure 7.100 and Table 7.4.

Distribution: *G. fischeri* is known from Hà Giang, Tuyên Quang and Bắc Kạn Provinces (Figure 7.116).

Remarks: Some shells from the Ba Bê National Park (Vn10-28A, 2009.05.17A, 2011/91, 2011/96) are indistinguishable from the type specimen of *Plectopylis tenuis* described from Cho Ra. This town is situated about 7 km from the locality of my recent material. About 3 km north of the *tenuis* localities there is a population (2009.05.15C) 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, I 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. The shells collected at Đồng Tiển are small and very shiny in appearance.

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

Figures 7.8, 7.44

- 1898b *Plectopylis Francoisi* Fischer, Journal de Conchyliologie, 46 (3): 214–218, Figs 1, 3–4. ["rochers calcaires Déo-Ma-Phuc"].
- 1899 *Plectopylis Francoisi* Fischer, Bulletin biologique de la France et de la Belgique, 32: 330–332, Figs 1, 3–4. ["rochers calcaires Déo-Ma-Phuc"]
- 1899d *Plectopylis francoisi*, — Gude, Science Gossip, 6: 75–76. Figs 201a–e.
- 1899e *Plectopylis (Endoplon) francoisi*, — Gude, Science Gossip, 4: 148.
- 1899f *Plectopylis (Endoplon) francoisi*, — Gude, Science Gossip, 6: 175.
- 1900 *Plectopylis lepida* Gude **new synonym**, The Annals and magazine of natural history 7 (5): 313. ["Tonkin, Tinh-Tuc"].
- 1901b *Plectopylis Bavayi* Gude **new synonym**, Journal de Conchyliologie, 49: 200–202., Figs 2a–e., Plate 6, Figs 2a–c. [That Khé (le type); secteur de Nac-Ri]
- 1901c *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.
- 2015 *Gudeodiscus (Gudeodiscus?) francoisi*, — Páll-Gergely et al., Zookeys 472: 26, Figs 7A–C, 13E–K.

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

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. Messenger, MNHN-IM-2012-2227/6; Tonkin, leg. Messenger, MNHN-IM-2012-2229/4; Tonkin, coll. Letellier 1949, MNHN-IM-2012-2267/1; Secteur de Nac-Ri, leg. Messenger, MNHN-IM-2012-2268/5; That-Khé, coll. Lavezzari, 1929, MNHN-IM-2012-2276/5; Tonkin, leg. Messenger, MNHN-IM-2012-2284/1; That Ké, Nac Ri, leg. Messenger, MNHN-IM-2012-2333/8; Tonkin, leg. Messenger, MNHN-IM-2012-2353/1; Na-Cham, leg. Messenger, MNHN-IM-2012-2358/5; Na-Ri, leg. Messenger, MNHN-IM-2012-2363/5; Tonkin, leg. Messenger, MNHN-IM-2012-2428/1; Tonkin, leg. Messenger, MNHN-IM-2012-2440/6; Tonkin, leg. Messenger, MNHN-IM-2012-2430/7; Nac-Ri et That-Khe, coll. Staadt, 1969, MNHN-IM-2012-2386/2; Tonkin, leg. Messenger, MNHN-IM-2012-2371/3; That-Khé, leg. Messenger, MNHN-IM-2012-2377/30+3 juvenile shells; 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 Messenger, NHMW 92561/2; Tonkin, Phi-Mi, coll. Steenberg, ZMUC-1807/1; Tonkin, coll. Steenberg, ZMUC-GAS-1806/1.

New material examined: **GS17** Bắc Kạn Prov, Na Rì Distr., limestone cliffs on the left side of the road to Kim Hỷ, 2 km before Kim Hỷ, soil in small cavern, 558 m, 22°16'53.81"N, 106°02'45.24"E, leg. Grego, J. & Šteffek, J., 05.04.2012., PGB/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, 587 m, 22°14'32.81"N, 106°00'31.65"E, leg. Grego, J. & Šteffek, 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, 637 m, 22°14'30.36"N, 106°00'31.27"E, leg. Grego, J. & Šteffek, J., 06.04.2012., 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.

Differential diagnosis: The shiny, 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* (Đèo-Ma-Phuc) 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*. I cannot exclude the possibility of hybridisation in that locality, however specimens from other localities are easily distinguishable.

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).

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: I was able to study newly-collected material from Cao Bằng and Bắc Kạn Provinces. There is a single shell which is very similar to the holotype of *Plectopylis lepida* and is labelled as being collected from Hạ Long Bay, but this collection locality is probably incorrect (Figure 7.117).

Remarks: *G. bavayi* is a synonym of *G. francoisi*. The two holotypes are very similar in shell shape and arrangement of the inner lamellae. The only difference is that the holotype of *G. francoisi* lacks an apertural fold in the aperture because it is a subadult shell. Other shells collected from the type locality are indistinguishable from 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, I 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*, I treat the former as the junior synonym of *Plectopylis francoisi*.

***Gudeodiscus (Gudeodiscus) giardi* (H. Fischer 1898)**

Diagnosis: A middle sized/large *Gudeodiscus* species with domed apical region, deep but moderately wide umbilicus, conspicuously oblique aperture and very much thickened peristome. On the parietal side the lower horizontal plica is in contact with the anterior lamella.

Differential diagnosis: The species most similar to *Gudeodiscus giardi* is *G. francoisi*. For comparisons, see under this species. *G. dautzenbergi* is larger, flatter, has narrow umbilicus, weaker apertural lip and the lower end of the anterior lamella is very much elongated anteriorly. *G. villedaryi* is also flatter; most populations have a keel around the umbilicus and have an additional long plica below the parietal lamellae. *G. 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 elevated spire, but their shell shape is rather conical, whereas it is usually domed (rounded) in *G. giardi*.

***Gudeodiscus (Gudeodiscus) giardi giardi* (H. Fischer 1898)**

Figures 7.6, 7.7, 7.48, 7.49, 7.62, 7.63, 7.90, 7.91, 7.94, 7.95, 7.100, 7.133

- 1898a *Plectopylis Giardi* Fischer, Bulletin Biologique de la France et de la Belgique, 28: 320–322, pl. 17, Figs 17–21. ["Cao-Bang"].
- 1898b *Plectopylis Giardi* Fischer, Journal de Conchyliologie, 46 (3): 214–218, Figs 2, 5–6. ["rochers calcaires Déo-Ma-Phuc"].
- 1899a *Plectopylis Giardi* Fischer, Bulletin biologique de la France et de la Belgique, 32: 330–332, Figs 2, 5–6.
- 1899b *Plectopylis giardi*, — Gude, Science Gossip, 5: 332–333, Figs 95a–e ["Cao-Bang, Tonkin"].
- 1899b *Plectopylis congesta* Gude **new synonym**, Science Gossip, 5: 332–333. Figs 96a–f. ["Tonkin", "Its exact locality, unfortunately, was not stated."]
- 1899d *Plectopylis giardi*, — Gude, Science Gossip, 6: 76, fig. 103.
- 1899e *Plectopylis (Endoplon) giardi*, — Gude, Science Gossip, 4: 148.
- 1899e *Plectopylis (Endoplon) congesta*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Endoplon) giardi*, — Gude, Science Gossip, 6: 175.
- 1899f *Plectopylis (Endoplon) congesta*, — Gude, Science Gossip, 6: 175, 176.
- 1901b *Plectopylis congesta*, — Gude, Journal de Conchyliologie, 49: 199, 202, 209, 211–212. ["Entre Bac-Kan, et Nac-Ri; environs de Bac-Kan; That-Khé"]
- 1908b *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).
- 2014a *Gudeodiscus giardi giardi*, — Páll-Gergely & Asami, Genus 25(3): 536, Figs 9, 20D.
- 2015 *Gudeodiscus (Gudeodiscus) giardi giardi*, — Páll-Gergely et al., Zookeys 472: 28, Figs 7E–F, 8A, 9I, 13L–U, 19, 28B, 29E, 30D, 32C, 35A–C, 45A.

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

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. Messenger (n. 28), RBINS/1; Tonkin, Long-Phai, NHMSB 122815/1; Long-Phai, leg. Messenger, 1901, MNHN-IM-2012-2231/13; Nga-Son, leg. Messenger, MNHN-IM-2012-2235/1; Long-Phai, leg. Messenger, 1901, MNHN-IM-2012-2236/16; Quang-Huyen, leg. Mansuy, MNHN-IM-2012-2238/14; Bac-Kan, leg. Messenger, MNHN-IM-2012-2239/7; That-Khé, leg. Messenger, MNHN-IM-2012-2240/9; Bac-Kan, leg. Messenger, 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. Staat, 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. Lavezzari, 1929, MNHN-IM-2012-2309/3; That-Khé, leg. Messenger, MNHN-IM-2012-2310/6; Cao-Bang, leg. Messenger, MNHN-IM-2012-2469/7; Tonkin, leg. Messenger, MNHN-IM-2012-2460/9; Tonkin, leg. Messenger, MNHN-IM-2012-2441/1; Halong Bay, leg. Messenger, MNHN-IM-2012-2318/1; Halong Bay, leg. Messenger, MNHN-IM-2012-2319/1; Halong Bay, leg. Messenger, MNHN-IM-2012-2323/1; Tonkin, Bac-Kan, Na-Ri, leg. Messenger, MNHN-IM-2012-2324/47; That Khé, leg. Messenger, MNHN-IM-2012-2326/3; Po Ma, leg. Messenger, MNHN-IM-2012-2328/7; That Khé, coll. Staat 1969, MNHN-IM-2012-2330/3; That Khé, leg. Messenger, MNHN-IM-2012-2341/28; Po Ma, leg. Messenger, MNHN-IM-2012-2342/6; Cold de Nuages, leg. Messenger, MNHN-IM-2012-2343/4; Bac-Kan, leg. Messenger, MNHN-IM-2012-2344/8; Tonkin, leg. Messenger, MNHN-IM-2012-2345/8; That Khé, leg. Messenger, MNHN-IM-2012-2346/5; Cold de Nuages, leg. Messenger, MNHN-IM-2012-2349/4; Quang-Huyen, coll. Staat, 1969, MNHN-IM-2012-2351/1; Tonkin, leg. Messenger, MNHN-IM-2012-2352/10; Tonkin, leg. Messenger, MNHN-IM-2012-2355/1; Na-Cham, leg. Messenger, MNHN-IM-2012-2356/10; Na-Cham, leg. Messenger, MNHN-IM-2012-2357/5; Cao-Bang, leg. Messenger, MNHN-IM-2012-2359/4; That-Khé, leg. Messenger, MNHN-IM-2012-2374/4; Tinh Tuc, secteur de Nguyen Binh, coll. Achat Boubée, MNHN-IM-2012-2385/1; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2393/1; Tonkin, coll. Jousseau, MNHN-IM-2012-2399/1; Bac-Kan, leg. Messenger, MNHN-IM-2012-2432/1; Tonkin, leg. Messenger, MNHN-IM-2012-2426/3; Bac-Kan, leg. Messenger, MNHN-IM-2012-2435/1; Tonkin, coll. Lucas, Acc. no. 2351, NHMUK 20130604/2 ("*persimilis*"); Tonkin, 3/10/08, NHMUK 20130605/2 ("*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 ("*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 Messenger, NHMW 71640/O/10289/1; Tonkin, Ngan-Son, coll. Wagner ex Messenger, NHMW 71640/O/10288/1; Tonkin, Phi-Mi, NHMW 46023/2; Tonkin, Long-Phai, NHMW 46294/2; Tonkin, That-Khe, coll. Wagner ex Messenger, NHMW 71640/O/10286/1; Tonkin, Po-Ma (?), coll. Wagner ex Messenger, NHMW 71640/O/10287/1; Tonkin, Bac-Khuon, coll. Rolle, NHMW 103352/1 (mixed sample with *phylarius*); Tonkin, Quang-Huyen, coll. Steenberg, ZMUC-GAS-1813/2.

New material examined:

China: Guangxi, Daxin Xian, Yanlong Zhen, Touxian Cun, Cantun, 248 m, 22°51.73844'N, 106°49.43935'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 11.1.2006, OK/11, PGB/3; Guangxi, Daxin Xian, Yanlong Zhen, 4 km from (? road) No. 19, 310 m, 22°46.90712'N, 106°50.49314'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 11.1.2006, OK/7, PGB/3; Guangxi, Longzhou Xian, Nonggang Baohuqu (Protected Area), inside of the ranger station, 173 m, 22°28.13390'N, 106°57.63413'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 11.1.2006, OK/5, PGB/2; Guangxi, Longzhou county, Shuikou town, 200 m, 22°20'N, 106°45'E, leg. Dengxin, PGB/2; Guangxi, Longzhou Xian, Wude Xiang, Wude, 201 m, 22°28.50938'N, 106°47.67450'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 11.1.2006, OK/6, PGB/3; Guangxi, Daxin Xian, Yanlong Zhen, Jiangjun Shan, 267 m, 22°49.04890'N, 106°49.33238'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 11.1.2006, SMF 341508/1, OK/35, PGB/4; Guangxi, Napo Xian, Pohe Xiang, along the road to Longhe (pond during the rainy season?), 1195 m, 23°21.39313'N, 105°55.41642'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.1.2006, OK/1; **Deng1** Guangxi, Shuikou town, Longzhou county, about 200 m, 22°20'N, 106°45'E, leg. Dengxin, PGB/1; Guangxi, Longzhou Xian, Jinlung Zhen, Gaoshan Cun, Banloutun, 333 m, 22°43.51930'N, 106°47.36219'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 11.1.2006, OK/4, PGB/1; Guangxi, Longzhou Xian, ex coll. Hemmen, WM/1; Guangxi, Bose Shi, Lingyun Xian, Lingyun (Sicheng Zhen), Nalingdong, rocks next to the cave, 470 m, 24°21.923'N, 106°33.902'E, leg. Hunyadi, A., 19.10.2009, HA/1; Guangxi, Longzhou Xian, Nonggang Protected Area, near ranger station, 205 m, 22°28.48990'N, 106°57.43325'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 12.01.2006., OK/2; Guangxi, Longzhou Xian, near Nonggang, 202 m, 22°29.31403'N, 106°57.31251'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 12.01.2006., OK/4; Guangxi, Longzhou Xian, Nonggang Protected Area, inner side of ranger station, 173 m, 22°28.13390'N, 106°57.63413'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 12.01.2006., OK/6.

Vietnam: **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, 387 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 Rào., 544 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. ("*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 Phây (pass), Thát Khê N 13 km, 475 m, 22°20.363'N, 106°27.098'E, leg. Hunyadi, A., 15.11.2011., HA/8, PGB/1 ("*congesta*"); **2011/83** Cao Bằng Province, Đèo Lũng Phây (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 ("*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); **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 ("*congesta*"); **2011/84** Cao Bằng Province, Đông Khê 3 km towards Đèo Lũng Phây (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 ("*congesta*").

Diagnosis: A very variable *Gudeodiscus* subspecies with domed apical region, deep but moderately wide umbilicus and conspicuously oblique aperture. Apertural fold not in contact with the elevated callus; on the parietal side the lower horizontal plica is in contact with the anterior lamella.

Description: Shell domed; light brownish or yellowish; very finely, irregularly ribbed, with a fine spiral sculpture; this structure is also visible, although less prominent on the ventral side; umbilicus very deep but moderately wide; 8–9 regularly growing whorls are dense; separated by shallow suture; aperture oblique, lip conspicuously thickened and reflected; callus S-shaped; elevated; usually as thick and high as the apertural rim; short apertural fold free from the callus.

More than ten specimens were opened belonging to Chinese and Vietnamese populations. Parietal wall with two lamellae; anterior lamella very strong and high; with horizontal support above and below; posterior lamella well developed, longer and slimmer than the first one; on the palatal side the first and last plicae are more or less straight and parallel with the sutures; second, third and fourth plicae are complicated; Z-shaped, usually with additional pliculae posteriorly.

Differential diagnosis: *Gudeodiscus giardi giardi* differs from *G. giardi szekeresi* in the apertural fold, which is in contact with the callus in *szekeresi*, but free in the nominotypical subspecies. The lower horizontal plica is attached to the anterior lamella at a much larger angle in *G. giardi szekeresi*. *G. giardi oharai* has a much more depressed shell with a wider umbilicus and thicker apertural lip and fold, which is also connected with the lip as in *szekeresi*.

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).

Intraspecific diversity: Two subspecies of *G. giardi* were described from China (see Páll-Gergely & Hunyadi, 2013). The populations assigned to the nominotypical subspecies show larger variability in China in terms of shell size, shape, and morphology of plicae, 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).

Characters of the genital structure: One Chinese specimen was anatomically examined, which had no embryos in its uterus. Ethanol-preserved body is deposited in coll. PGB, respective shell in coll. JUO. Locality information: Guangxi, Longzhou Xian, Wude Xiang, Qunhe Cun, Banxintun, 308 m, 22°35.46563'N, 106°46.29486'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 11.01.2006.

The right ommatophoral retractor crosses the male and female genitalia. Penis very long, club-shaped with long, slender, proximal portion and thickened distal "head"; penial caecum moderately long, slightly shorter than the epiphallus; epiphallus slender, approximately as long as the thickened distal part of the penis. Penis internally with longitudinal folds, in some parts with hardly visible reticulated sculpture; the inner wall of the distal end of the penis had several longitudinal slit-like "pockets", which contained flat, thin, calcareous crystals (one crystal per pocket). Distal end of the penis and the proximal part of the penial caecum had reticulated sculpture. The inner wall of the penial caecum was tuberculated, the tubercles were standing in pairs; probably forming pockets for calcareous crystals, as it was visible in *G. pulvinaris pulvinaris* (see below). Epiphallus internally with longitudinal folds. Vas deferens very long, curly; thickened near its insertion to the spermoviductus. Vagina very long, approximately as long as the penis and penial caecum together, it has well-developed vaginal bulb at its proximal part. Gametolytic sac and the additional organ next to it are very long and slender; the gametolytic sac had a thickened distal end.

A single Vietnamese specimen was anatomically examined. 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. 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; 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; epiphallus C-shaped, longer than the penis; its inner wall with three longitudinal parallel folds; penis and epiphallus connected with weak membrane; penial caecum about 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; gametolytic sac and diverticulum slender, they are about the same length.

Radula: Figure 7.100 and Table 7.4.

Distribution: Newly-collected material was examined from Cao Bằng Province and the northern part of Lạng Sơn Province. This species is also known from the western part of Guangxi, China (Figure 7.117).

Remarks: *Gudeodiscus giardi* is very variable in terms of shell size, colour and sculpture. The characteristic features of the species are the following: deep, moderately wide umbilicus, free apertural fold and the anterior lamella is connected to the lower plica. The population collected from Pohe Xiang has a translucent, yellowish shell, lacking spiral structure dorsally. The ventral side is smooth. The shells from Cantun show intermediate characters between *G. giardi giardi* and *G. giardi oharai*; they possess an apertural fold free from the callus and the shells are dark, similar to those of the nominotypical subspecies. They have however, a relatively flat shell with a wider umbilicus as seen in *G. giardi oharai*. A single shell collected from Nalingdong is flatter than the typical *giardi* specimens.

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 posterior lamella and the anterior lamella which is fused to the upper parietal plica. This population however, falls within the morphological range of the very variable *G. giardi giardi*, therefore *P. congesta* is here synonymised with *G. giardi giardi*.

***Gudeodiscus (Gudeodiscus) giardi oharai* Páll-Gergely 2013**

Figures 7.7, 7.48

2013 *Gudeodiscus giardi oharai* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 20, Figs 30, 54a–b.

Type material: Guangxi, Wuming Xian, Shuangqiao Zhen, Xianshanyuan, 177 m, 23°02.08015'N, 108°17.68551'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 17.6.2005, holotype HNHM 97449, paratypes HA/1, OK/18, PGB/3; Guangxi, Wuming Xian, Shuangqiao Zhen, Yiqiang, near the highway entrance opposite to gas station, 159 m, 23°01.51429'N, 108°17.95496'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 17.6.2005, OK/3; Guangxi, Wuming Xian, Shuangqiao Zhen, Yiqiyan, 115 m, 23°02.48524'N, 108°17.69805'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 17.6.2005, NHMW 108167/1, OK/32, PGB/3; Guangxi, 10 km N of Nanning, leg. Shiro Hisano, May 2001, ex coll. Hemmen, J., SMF341509/1, PGB/2, same data, ex coll. Maassen, W., PGB/1, WM/2.

Diagnosis: A small, yellowish, translucent *Gudeodiscus* subspecies with oblique aperture having very thick, slightly reflected lip. The apertural fold is in contact with the conspicuously elevated callus.

Description: Shell depressed conical/discoid; with only slightly elevated spire; yellowish; thin, translucent; the 7–7.5 whorls are separated by shallow suture; umbilicus very deep and wide; aperture oblique; with a very well-developed and slightly reflected lip; apertural fold long and high; it is in contact with the elevated callus.

Three specimens were opened. Since the shell was so thin, the parietal lamellae were visible without breaking the shell. Parietal wall bears two strong lamellae; the anterior one in contact with the lower horizontal lamella, but free from the upper one; lower horizontal lamella and the anterior vertical lamella join underneath at a large angle; in one of the opened specimens the horizontal lamella almost continues the line of the vertical plate; on the palatal side two horizontal plicae are present (one on the lower side and one above); between these are three major vertical plicae; sometimes with additional pliculae; these plicae can be simple or with a dichotomic branching at the lower end.

Differential diagnosis: *Gudeodiscus giardi oharai* differs from the nominotypical subspecies by the more depressed, usually smaller, translucent and yellowish shell. *G. giardi oharai* has a thicker apertural lip with more elevated callus than *G. giardi giardi*. Additionally, the apertural fold is in contact with the callus. *G. giardi szekeresi* is larger, has a thicker and darker shell, its apertural lip is not reflected and the callus is lower. *G. giardi oharai* differs from the other *Gudeodiscus* taxa from Guangxi by the very thick apertural lip and the strong apertural fold.

Measurements (in mm): D= 11.6–15.3, H= 5.5–6.8 (n=6).

Etymology: This subspecies is dedicated to Kenji Ohara, the collector. His contribution was very important to this revision.

Type locality: Guangxi, Wuming Xian, Shuangqiao Zhen, Xianshanyuan, 177 m, 23°02.08015'N, 108°17.68551'E.

Distribution: This subspecies is known only from a small area north of Nanning, Western Guangxi (Figure 7.117).

Remarks: See under *G. giardi giardi*.

***Gudeodiscus (Gudeodiscus) giardi szekeresi* Páll-Gergely & Hunyadi 2013**

Figures 7.7, 7.48

2013 *Gudeodiscus giardi szekeresi* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 21, Figs 29, 55a–d.

Type material: Guangxi, Chongzuo Shi, about 25 km SE of Chongzuo, Chongzuo Shengtai Gongyuan, Langur Reserve (Fusui Rare Animal Protection Station), 220 m, 22°16.293'N, 107°30.359'E, leg. Hunyadi, A., 18.10.2009, holotype HNHM 97450, paratypes HA/3, PGB/2.

Diagnosis: A middle-sized, brownish *Gudeodiscus* subspecies with deep but moderately wide umbilicus and oblique aperture possessing a very thick, non-expanding lip. The apertural fold is in contact with the elevated callus.

Description: Shell brownish; depressed conical-discoid with only slightly elevated spire; although it presents a robust impression, the shell wall is rather thin; the 8–8.5 whorls are separated by shallow suture; umbilicus deep but moderately wide; about one third of the shell width; aperture oblique, with a very well-developed but non-reflected lip; apertural fold relatively long and high; in contact with the elevated callus.

Two specimens were opened. Parietal wall with two strong lamellae; anterior in contact with the lower horizontal lamella, but free from the upper one; the lower horizontal lamella and the anterior vertical lamella join at a large angle; on the palatal side there are two horizontal plicae on the upper side and one below; between these there are three major vertical plicae; sometimes with additional pliculae; plicae can be simple or dichotomously subdivided at their lower ends.

Differential diagnosis: *G. giardi szekeresi* differs from the nominotypical subspecies by the more depressed shell, the less reflected apertural lip that is continuous with the callus, and the apertural fold, which is in contact with the callus. The lower horizontal plica joins the anterior lamella at the larger angle. *G. giardi oharai* is smaller, has a wider umbilicus, more conspicuous and expanding apertural lip with a higher callus, and has thinner, translucent shell.

Measurements (in mm): D = 18.3, H = 8.9 (holotype).

Etymology: This subspecies is dedicated to the clausiliid specialist and much-valued friend, Miklós Szekeres.

Type locality: Guangxi, Chongzuo Shi, about 25 km SE of Chongzuo, Chongzuo Shengtai Gongyuan, Langur Reserve (Fusui Rare Animal Protection Station), 220 m, 22°16.293'N, 107°30.359'E.

Distribution: *G. giardi szekeresi* is known only from the type locality in southern Guangxi (Figure 7.117).

Remarks: The available material mainly contains corroded, chalky shells.

***Gudeodiscus (Gudeodiscus?) hemmeni* Páll-Gergely & Hunyadi 2015**

Figures 7.15, 7.42

2015 *Gudeodiscus (Gudeodiscus?) hemmeni*, — Páll-Gergely et al., Zookeys 472: 32, Figs 2C–D, 9F, 11G–J.

Type material: **2012/61** Son 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, HA/11 paratypes+4jb (not paratype), PGB/3 paratypes; **2012/62** Son 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** Son 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; **Vn10-76A** Son 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 sinus, and small apertural fold; 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.

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) shiny, 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 exceed the lamella anteriorly. Palatal side with six plicae; first and last are straight, the others are depressed Z-shaped and are connected with a ridge.

Differential diagnosis: 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. *G. anceyi* is usually smaller, has longer apertural fold, prominent spiral sculpture, weaker callus and differently shaped aperture.

In all localities, *G. hemmeni* u. sp. lives sympatrically with *G. messengeri raheemi* u. ssp., which is much larger, lacks the apertural fold, and usually has a dissolved anterior lamella.

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

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

Etymology: This new species is dedicated to Jens Hemmen (1944–2012), malacologists and much-valued friend, who contributed in our revision with providing shell and ethanol-preserved material.

Distribution: *Gudeodiscus hemmeni* u. sp. is known from few locations in south-eastern Son La province (Figure 7.119).

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

Figures 7.9, 7.46

1908b *Plectopylis infralevis* Gude, Journal de Conchyliologie, 55: 345, 350, 352–353. Figs 3a–e., Plate 7, Figs 4–6. ["Quang Huyen"]

1908b *Plectopylis soror* Gude **new synonym**, 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.

2015 *Gudeodiscus (Gudeodiscus?) infralevis*, — Páll-Gergely et al., Zookeys 472: 34, Figs 3D–E, 15A–D.

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

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.

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 (*G. 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*. For comparison with *G. suprafilaris* see there.

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

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 material of *Plectopylis infralevis* and *P. soror* (synonym of *infralevis*) were collected in Quang Huyen (Quảng Uyên) (Figure 7.109).

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* and 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, because no other species of Plectopylidae have three lamellae. The differences between the two specimens suggest intraspecific variance. Unfortunately I have no freshly-collected material of these two forms, but because of the high similarity between the two holotypes and same type locality I here synonymise *soror* with *infralevis*. These two names were published in the same paper (Gude 1908b), but *infralevis* was described earlier in terms of page numbers.

***Gudeodiscus (Gudeodiscus?) marmoreus* Páll-Gergely 2014**

Figure 7.17, 7.49

2014a *Gudeodiscus marmoreus* Páll-Gergely in Páll-Gergely & Asami, Genus 25(3): 536–537, Figs 1, 5C, 5E.
2015 *Gudeodiscus (Gudeodiscus?) marmoreus*, — Páll-Gergely et al., Zookeys 472:13.

Material: China, Guangxi, Hechi city, east of BaMa Xian, ex coll. Yang Hao, 2013, HNHM 97457 (holotype).

Diagnosis: A very large, flat species with a low, long fold in the aperture which is free from the callus. Dorsal surface with coarse radial ribs and very fine spiral lines. On the parietal wall there are two lamellae with horizontal plicae above and below the anterior lamella.

Description of the holotype: Shell brownish with lighter mosaic colouration dorsally and a yellowish band around the umbilicus, which is visible in all whorls inside the infundibular umbilicus; shell flat with a slightly elevated apex; 7.5 whorls are separated by rather shallow suture; protoconch very finely, regularly ribbed; dorsal surface of teleoconch with extremely fine, microscopic spiral lines and coarse, irregular radial growth lines; shell surface almost smooth around the umbilicus; within the umbilicus spiral lines not visible, only the radial growth lines; peristome brown, thickened and reflexed, with slightly S-shaped, low callus and a white, low entering fold free from it.

The armature is situated very deep, about half whorl behind the aperture; parietal wall with two lamellae; anterior one rather straight and short, above slightly elongated anteriorly, below both anteriorly and posteriorly; posterior lamella long and very much curved; two horizontal plicae are above and below the first lamella, the lower one starts from the lower end of the posterior lamella and stops at the middle of the anterior lamella; the upper plica is about as long as lower, starts just anterior to the posterior lamella, and it exceeds the anterior lamella. Palatal wall with six plicae; first long and slim, close to the suture and situated posterior of the other plicae; second bent posteriorly; third and fourth almost vertical, slightly depressed Z-shaped; fifth short and V-shaped, probably consists of two plicae; the sixth one is situated anterior of the other plicae, slim; there are two additional small, denticle-like plicae posterior to the fifth and sixth plicae.

Differential diagnosis: The coloration (mosaic structure dorsally, light band around the umbilicus) and the sculpture (extremely fine spiral lines and rough radial growth ridges) of *G. marmoreus* is unique among *Gudeodiscus*.

Moreover, most large, flat species reported from China ("*Chersaecia*" *andersoni* (Blanford 1869), *G. concavus* Páll-Gergely 2013, *G. eroessi* Páll-Gergely 2013, *Gudeodiscus goliath* Páll-Gergely & Hunyadi 2013, *G. okuboi* Páll-Gergely & Hunyadi 2013, *G. pulvinaris* (Gould 1859)) have only one parietal lamella. Some taxa however, have two parietal lamellae (*G. emigrans otanii* Páll-Gergely 2013, *G. giardi*, *G. phlyarius*, *G. yanghaoi* Páll-Gergely & Hunyadi 2013). These differ from the *G. marmoreus* in the following shell characters: *G. emigrans otanii* has Y-shaped palatal plicae, sometimes four parallel plicae instead of an anterior lamella in front of the lamella and has fine ribbing on the whole shell. *G. giardi* and its subspecies have the more elevated spire, domed shell shape and their anterior lamella is connected to the lower plica. *G. phlyarius* usually has the more elevated spire, stronger apertural fold, thicker peristome and finely ribbed sculpture than *G. marmoreus*. *G. yanghaoi*, which is probably the closest relative to *G. marmoreus*, has the more elevated spire, a long entering fold connected to the callus, all middle palatal plicae are united and being visible as one plate through the semitransparent shell, which has the finely ribbed dorsal surface.

Measurements (in mm, holotype): D=26.7, H=9.6.

Etymology: This species is named after its marbled dorsal shell surface (marmoreus = marbled in Latin).

Distribution: Only the holotype is known from the type locality (Figure 7.108).

Gudeodiscus (Gudeodiscus) messengeri (Gude 1909)

Diagnosis: Shell small to medium-sized, with slightly elevated spire, apex somewhat domed; aperture almost circular, apertural fold missing; callus not sharpened and only slightly curved. Parietal wall with two lamellae (the anterior lamella may be dissolved); 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) messengeri messengeri (Gude 1909)

Figures 7.15, 7.43

1909 *Plectopylis messengeri* Gude, Proceedings of the Malacological Society of London, 8: 214, 215, pl. 9, Figs 4, 4a–b. ["Moung-Hum", "Nat-Son, Pac-Kha, and Trinh-Tuong"]
2013 *Gudeodiscus messengeri*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 8.
2015 *Gudeodiscus (Gudeodiscus) messengeri messengeri*, — Páll-Gergely et al., Zookeys 472: 35, Figs 5F–G, 9E, 12N–Q.

Types examined: Tonkin, Muong-Hum, leg. Messenger, HNMIK 1922.8.29.53 (holotype), Tonkin, Nat-Son, leg. Messenger, NHMIK 1922.8.29.54 (holotype of *messengeri* var. *minor*).

Museum material examined: Tonkin, coll. Dosch ex Rolle ex Messenger, 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 Messenger, 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 Messenger, SMF 182088/4; Tonkin, Ba-Nat (?), NHMSB 131/200, 122812-122813 (2 shells); Pakhé, leg. Messenger, MNHN-IM-2012-2129/9; Muong-Hum, leg. Messenger, MNHN-IM-2012-2134/15; Nat-Son, Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2136/16 ("var. *minor*"); Muong-Kong, leg. Messenger, MNHN-IM-2012-2137/4; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2142/2 adult, 4 juvenile shells; Muong-Hum, leg. Messenger, MNHN-IM-2012-2131/5; Muong-Hum, leg. Messenger, MNHN-IM-2012-2143/3; Muong-Hum, leg. Messenger, MNHN-IM-2012-2145/74; Pakhé, leg. Messenger, MNHN-IM-2012-2149/1; Pac-Kha (Pakhé), leg. Messenger, MNHN-IM-2012-2151/10; Nat-Son, leg. Messenger, MNHN-IM-2012-2154/6; Muong-Kong, leg. Messenger, MNHN-IM-2012-2159/1; Nat-Son, leg. Messenger, MNHN-IM-2012-2162/29; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2163/20; Nat-Son, leg. Messenger, MNHN-IM-2012-2165/8 adult, 25 juvenile shells; Bac-Kan, leg. Messenger, MNHN-IM-2012-2166/6; Bac-Kan, leg. Messenger, MNHN-IM-2012-2172/4; Muong-Hum, leg. Messenger, MNHN-IM-2012-2173/3; Muong-Hum, leg. Messenger, MNHN-IM-2012-2183/4; Pakhé, leg. Messenger, MNHN-IM-2012-2184/1; Long-Ping, leg. Messenger, MNHN-IM-2012-2186/8; Muong-Hum, leg. Messenger, MNHN-IM-2012-2188/8; Bac-Kan, leg. Messenger, MNHN-IM-2012-2194/3; Muong-Hum, leg. Messenger, MNHN-IM-2012-2196/4; Nat-Son, leg. Messenger, MNHN-IM-2012-2198/2; Nat-Son, leg. Messenger, MNHN-IM-2012-2199/2; Tonkin, leg. Messenger, MNHN-IM-2012-2202/1; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2205/12; Muong-Kong, leg. Messenger, MNHN-IM-2012-2479/1; Bac-Kan, leg. Messenger, MNHN-IM-2012-2475/10; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2472/16; Cao-Bang, leg. Messenger, MNHN-IM-2012-2471/1; Tonkin, Pakhé, leg. Messenger, MNHN-IM-2012-2458/7; Long-Ping, leg. Messenger, MNHN-IM-2012-2457/23; label not readable, leg. Messenger, MNHN-IM-2012-2449/2; Bac-Kan, leg. Messenger, MNHN-IM-2012-2403/1; Trinh-Thuong, coll. Lavezzari, 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. Messenger, MNHN-IM-2012-2425/3; Gia-Phu, leg. Messenger, MNHN-IM-2012-2215/33; Muong-Hum, leg. Messenger, MNHN-IM-2012-2216/3; Long-Ping, leg. Messenger, MNHN-IM-2012-2217/9; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2219/12; Col de Nuages, leg. Messenger, MNHN-IM-2012-2221/1; Trinh-Tuong, leg. Messenger, MNHN-IM-2012-2223/2; Tonkin, leg. Messenger, MNHN-IM-2012-2225/4; Tonkin, leg. Messenger, MNHN-IM-2012-2230/1; Long-Phai, leg. Messenger, 1901, MNHN-IM-2012-2237/2; Muong-Kong, leg. Messenger, 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. Messenger, MNHN-IM-2012-2339/1; Bac-Kan, leg. Messenger, MNHN-IM-2012-2315/1; Gia-Phu, leg. Messenger, MNHN-IM-2012-2364/2; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2379/1; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2394/1; Tonkin, Pac-Kha, NHMIK 1916.3.16.15/1; Tonkin, Pac-Kha, coll. Kennard, A.S. ex auct. (Gude), NHMIK 20130620.2/1; Tonkin, Muong-Hum, coll. Biggs, H.E.J. ex Gyngell, 1930, Acc. no. 2258, NHMIK 20130626/2; Tonkin, Gia-Phu, coll. Kennard, A.S. ex auct. (Gude), NHMIK 20130627/2; Tonkin, Muong-Kong, coll. Salisbury ex Beddome, NHMIK 20130628/2; Tonkin, Muong-Kong, 31/3/09, NHMIK 20130629/3; Tonkin, Muong-Hum, 5/1/09, NHMIK 20130630/3; Tonkin, Pac-Kha, 3/11/08, NHMIK 20130631/2 ("var. *minor*"); Tonkin, 5/1/09, NHMIK 20130632/3; Tonkin, Muong-Hum, coll. Preston, NHMIK 20130633/2; Tonkin, Muong-Bo, 3/11/08, NHMIK 20130634/2 ("var. *major*"); Tonkin, That-Khé, coll. Salisbury ex Beddome, NHMIK 20130635/1; Tonkin, Muong-Hum, coll. Kennard, NHMIK 20130636/1; Tonkin, Muong-Hum, NHMIK 1909.3.17.29–31/3; Tonkin, Muong-Hum, NHMIK 1916.3.16.16–18/3; Tonkin, Pac-Kha, NHMIK 1909.3.17.32–34/3 ("var. *minor*"); Tonkin, Pac-Kha, NHMIK 1909.3.17.24–25/2; Tonkin, Muong-Bo, NHMIK 1909.3.17.35–36/2 ("var. *major*"); Tonkin, Gia-Phee, coll. Rušnov ex Rolle ex Messenger, NHMW 92576/1; Tonkin, Trisch-Tuong, coll. Edlauer ex Werner, NHMW 75000/E/7983/2; Tonkin, Muong-Hum, coll. Oberwimmer ex Wagner ex

Messenger, NHMW 92573/2; Tonkin, Bac-Kan, coll. Oberwimmer, NHMW 71640/O/14028/1; Tonkin, Long-Ping, 3000 m, coll Oberwimmer ex Wagner ex Messenger, NHMW 92572/1; Tonkin, Muong Hum, coll Rosen ex Messenger, 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 Messenger, NHMW 71640/O/9477/1; Tonkin, Trisch Tuong, coll. Rušnov ex Rolle ex Messenger, 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 (mixed sample with "*gouldingi*"); Tonkin, Nat-Son, coll Rušnov ex Messenger, NHMW 103355/1 (mixed sample with "*gouldingi*"); Vietnam/132, Lao Cai Province, Cox-Xan, 400 m, leg. Topál & Matskási, 27.11.1971., VA/10.

Diagnosis: Anterior lamella normal (not dissolved); lower parietal plica does not exceed the anterior palatal lamella.

Differential diagnosis: *Gudeodiscus messengeri messengeri* 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. This allows *G. messengeri* and *G. phlyarius* to be distinguished without breaking the shell. The lower parietal plica, which does not exceed the anterior lamella, is characteristic of *G. messengeri messengeri*, but extremely rare on "*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 exceeds the anterior lamella in anterior direction.

For comparison with *G. messengeri raheemi* u. ssp., see under that taxon.

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

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

Distribution: I was only able to study museum material which suggested that this species is located along the Chinese border (Figure 7.119).

Remarks: In one sample (MNHN-IM-2012-2215) a specimen had longer lower plica which exceeded the anterior lamella.

***Gudeodiscus (Gudeodiscus) messengeri raheemi* Páll-Gergely & Hunyadi u. ssp.**

Figures 7.15, 7.31, 7.64, 7.65, 7.91, 7.95, 7.101

2015 *Gudeodiscus (Gudeodiscus) messengeri raheemi*, — Páll-Gergely et al., Zookeys 472: 38, Figs 5D, 5E, 10A, 12R–V, 20, 28E, 29F–G, 31B, 35D–F.

Material:

Vietnam: **MAA10** Ninh Binh 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., PGB/1 paratype, WM/3 paratypes; **MAA1** Thanh Hóa Province, Pù Luông N. P., 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 N. P., 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** Son 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 data, leg. Hemmen, 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); **20080509C** Nghệ An Prov., Pù Mát Nat. Park, Con Cường Dist., Lục Dạ Commune, Tân Hợp Village, 92 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, 39 m, 20°19.92147'N, 105°12.49178'E, leg. Ohara, K., 2007.11.18., PGB/1 paratype; **20071118B** Thanh Hóa Province, Cây Đãng Cave, Lương Ngọc, Cẩm Lương C., (GPS not recorded), leg. Ohara, K., 18.11.2007., PGB/1 paratype; **20071116C** Ninh Binh Province, Cúc Phương Nat. Park, Cave of Prehistoric Man, 146 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. & J., 02.10.2012., HE/7 paratypes; same data, leg. Hemmen, 08.10.2010, PGB/2 paratypes; same data, leg. Hemmen, 14.10.2011., HE/17 paratypes; **2011/106** Ninh Binh Province, Cúc Phương Nat. Park, main entrance, 700 m towards Bồng 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 Binh 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 Đẳng (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 Prov., 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; **Vn11-215** Sơn La Prov., ca. 34 km from Mộc Châu to Mai Châu, 20°45.219'N, 104°54.458'E, leg. Hemmen, Ch., 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 Quỳnh Châu, 19°24.363'N, 105°26.521'E, leg. Hemmen, Ch., 22.10.2011., HE/1 paratype; **Vn12-268** Thanh Hóa Prov., km 585 on road 15 Yên Cát to Ngọc Lặc 1 km right off road 15, 19°45.589'N, 105°25.521'E, leg. Hemmen, Ch., 14.04.2012., HE/3 paratype.

Laos: 11L06, SE of Muang Xiang Ngeun ~ 18 km, on the left side of Nam Khan, Luang Prabang province, central Laos, Limestone, black soil in limestone pockets, clay. Under rocks and logs in old forest. 19°40.931'N; 102°19.743'E; alt. 455 m, 50x300 m, 30 October 2006, Ahmed Abdou, Igor V. Muratov.

Diagnosis: Anterior lamella normal or dissolved, if normal, the lower plica exceeds it anteriorly.

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) shiny, 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 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 exceeds the lamella anteriorly; 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.

Differential diagnosis: The lower parietal plica exceeds the anterior lamella, which is extremely rarely the case in the nominotypical subspecies. The anterior lamella was dissolved in many samples, which has never been observed in the nominotypical subspecies. The umbilicus of the new subspecies is narrower, it has more rounded whorls and sharper, more angled callus, than in most samples of *G. messengeri messengeri*.

G. messengeri raheemi u. ssp. lives sympatrically with an atypical form of *G. phlyariius* in Ninh Binh Province. *G. phlyariius* is flat and has apertural fold, whereas *G. messengeri raheemi* u. ssp. has somewhat elevated spire and always lacks the apertural fold. See also under *G. hemmeni* u. sp.

Measurements (in mm): D= 12.9–14.4, H= 6.2–7.5 (Vn10-76); D= 14.2–14.4, H= 6.8–7.9 (2007.11.16C); D= 12.1, H= 6 (n=1, Vn11-230); D= 16–17.9, H= 7.3–7.9 (n=3, Vn11.104).

Intraspecific diversity: Relatively variable; the colour, spire height, size and morphology of the palatal and parietal lamellae and plicae show considerable variability. See Table 7.6.

Characters of the genital structure: 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); “Specimen2”, Nghệ An Province, Pù Huông Nature Reserve, Con Cuong District, Anh Sơn, Hoi Sơn, ca 30 m, 18°57.11872'N, 105°02.63029'E, leg. Ohara, K, Okubo, K & Otani, J. U., Sang, 10.05.2008.

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 form characteristic “pockets”; 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 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; “Specimen2” had a few elongated and globular calcareous granules within the hollows; 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; gametolytic sac and diverticulum of the same length, both relatively slim, although the gametolytic sac is a bit swollen.

Radula: Figure 7.101 and Table 7.4.

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

Distribution: The new subspecies is known from several localities in Ninh Binh, Thanh Hóa, Sơn La, Hòa Bình and Nghệ An provinces (Figure 7.119).

Gudeodiscus (Gudeodiscus) multispira (Möllendorff 1883)

Figures 7.10, 7.47, 7.66, 7.90, 7.101

1883 *Plectopylis multispira* Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 10: 378, pl. 12, Fig. 10 [“in provincia sinensi Hunan vel Guang-dung” and “südlichen Hunan oder nordlichen Guang-dung”].

1886 *Plectopylis multispira*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 187.

1887 *Helix multispira*, — Tryon, Manual of Conchology, 2 (3): 158, pl. 33, Figs 27–28 [Prov. Hunan, China].

1896d *Plectopylis multispira*, — Gude, Science Gossip, 3: 181, Figs 27a–d.

1899e *Plectopylis (Sinicola) multispira*, — Gude, Science Gossip, 6: 149.

1899f *Plectopylis (Sinicola) multispira*, — Gude, Science Gossip, 6: 176.

1920 *Plectopylis (Sinicola) multispira*, — Gude, Journal of Molluscan Studies, 14 (2–3): 64, Figs 5a–d.

1939 *Plectopylis multispira*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112, pl. 11, Fig. 14.

2013 *Gudeodiscus multispira*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 21, Figs 29, 55a–d.

2014a *Gudeodiscus multispira*, — Páll-Gergely & Asami, Genus 25(3): 538, Figs 10, 20E.

2015 *Gudeodiscus (Gudeodiscus) multispira*, — Páll-Gergely et al., Zookeys 472: 13, Fig. 35G–I, Tables 3, 6.

Types examined: China: Hunan vel Guang-dung, Slg. Möllendorff, holotype SMF 9262a. The specimen interpreted as the holotype by Yen (1939) (SMF 9261) is the result of invalid type designation. The species was described on the bases of a single shell (SMF 9262), which measures 9.05 mm (according to Möllendorff 1883, 9 mm), but Yen’s specimen measures 10.5 mm.

Museum material examined: China: Dau-dshou, Hunan, Slg. Möllendorff, SMF 9261/1; China: Dau-dshou, Hunan, Slg. Möllendorff (+ Slg. O. Boettger ex Möllendorff, 1890), SMF 9262a/10; China: Dau-dshou, Hunan, Slg. Kobelt ex Möllendorff, SMF 9262b/2; China: Dau-dshou, Hunan, Slg. Jetschin 1928, ex Möllendorff, SMF 118132/1; N-Guangdung, Slg. C. Boschex H. Rolle, SMF 172105/2; China: Daudschou, K2.90, Coll. Rolle, NHMW 50855/2; China: Nord —Guangdung, Coll. Rušnov per H. Rolle ex coll. Möllendorff, NHMW/2; Hunan, China, ex Mus. Berlin (H. Rolle), NHMUK 1890.10.17.105–106/2; Hunan, coll. Rolle, RBINS/1; China, Dandshon, ex coll. Rolle, USNM 198284/2.

New material examined: 20041112E Guangxi, Lipu Xian, Qingshan Zhen, Qingshan, 252 m, 24°26.189’N, 110°20.008’E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 12.11.2004, OK/5, PGB/2; Guangxi, Guilin Shi, Lipu Xian, southern part of Lipu, 190 m, 24°28.909’N, 110°24.024’E, leg. Hunyadi, A., 14.10.2009, SMF 341510/1, HA/34, PGB/6; Guangxi, Guilin Shi, Yangshuo Xian, Yangshuo SW 8 km, Yueliangshan (Moon Hill), 350 m, 24°43.702’N, 110°28.047’E, leg. Hunyadi, A., 15.10.2009, HA/4, PGB/1; **2009/90** Guangxi, Guilin Shi, Yangshuo Xian, Xinping Zhen N 5 km, Lotus Cave, 160 m, 24°56.256’N, 110°33.190’E, leg. Hunyadi, A., 15.10.2009, HA/13, PGB/5; Guangxi, Guilin Shi, Guilin, northern side of Diecaishan, leg. Hunyadi, A., 16.10.2009, HA/3, PGB/2; **2010/41** Hunan, Yongzhou Shi, Lingling Qu, Dengjiachong, rocky wall, 125 m, 26°13.808’N, 111°35.907’E, leg. Hunyadi, A., 8.11.2010, HA/1; Guangxi, Yangshuo Xian, Gaotian Zhen, Yueliang Shan, 24°43.45’N, 110°28.32’E, leg. Ohara, K., Okubo, K. & Otani, J. U., 16.5.2010, OK/23, PGB/4; Guangxi, Yangshuo Xian, Gaotian Zhen, near the Hudiequan bridge, 24°44.45’N, 110°29.62’E, leg. Ohara, K., Okubo, K. & Otani, J. U., 16.5.2010, OK/8; Hunan, Yongzhou Shi, Fujiaqiao Zhen, Danyan, leg. Ohara, K., Okubo, K. & Otani, J. U., 13.5.2010, OK/1; Guangxi, Guilin Shi, Caoping Huizu Xiang, Guanyan, 25°03.33’N, 110°26.88’E, leg. Ohara, K., Okubo, K. & Otani, J. U., 15.5.2010, OK/2; Guangxi, Yangshuo Xian, Xingping Zhen, Laozhai Shan, leg. Ohara, K., Okubo, K. & Otani, J. U., 16.5.2010, OK/2; Guangxi, Guilin, Hill across Reed Flute Cave, 25.306585°N 110.263607°E, leg. Podani, J., 1991 October, PJ/8; Guangxi, Yangshuo, leg. Podani, J. PJ/1; Guangxi, Yangshuo Xian, Fuli Zhen, Xinzhai Cun, 118 m, 24°45.816’N, 110°34.131’E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/1;

Guangxi, Sanjiang Xiang, Jiahui Xiang, Luohanduyan, 238 m, 25°01.120'N, 110°53.961'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/5; Guangxi, Sanjiang Xiang, Pingan Xiang, Chuanyan, 153 m, 24°55.120'N, 110°48.979'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/1; Guangxi, Pingyue Xian, Ertang Zhen, north of Chaotianyan, 182 m, 24°37.577'N, 110°45.710'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/2; Guangxi, Pingle Xian, Ertang Zhen, in front of Chaotianyan, 168 m, 24°37.500'N, 110°45.474'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/4; Guangxi, Zhongshan Xian, Wanggao Zhen, Bishuiyan, 170 m, 24°35.992'N, 111°25.447'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/1; Guangxi, Yangshuo Xian, Puyi Xiang, Muqiao, 125 m, 24°43.590'N, 110°32.355'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/1; Guangxi, Yangshuo Xian, Yangshuo Zhen, Mushan, 126 m, 24°46.342'N, 110°31.301'E, leg. Ohara, K., Okubo, K. & Otani, J. U., JUO/3; Guangxi, Guilin Shi, Gongcheng Xian, Pingan Xiang, Jiaojintang, 750 m, 24°45.454'N, 110°53.530'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/2, PGB/1.

Diagnosis: A highly variable, small *Gudeodiscus* species with dense whorls, translucent shiny shell and an occasional denticle in the aperture. Parietal wall with one vertical lamella and usually four denticles before it (anteriorly).

Description: Shell light brown or corneous yellow; with slightly elevated spire, but sometimes almost flat; smooth on the ventral side, with irregular, wrinkled structure on the dorsal surface; despite this structural feature, the shell is still translucent and shiny; the 6.75–7.75 low, moderately increasing whorls are separated by shallow suture; umbilicus very wide and moderately deep; apertural rim white and thickened; more or less expanded; callus totally missing in some populations; in other populations it is almost as thick as the apertural lip; sometimes a small denticle is present however, it is never connected to the parietal callus.

Six specimens were opened, belonging to different populations. Parietal wall with a curved lamella, which can have a conspicuous breaking point on the lower side; anteriorly to the lamella two plicae above and below and two-three additional denticles in between; rarely, these additional denticles are joined into one vertical ridge, or they are missing in some specimens; palatal wall with six plicae; first rarely missing; first plica close to the suture, usually very weak; second, third, fourth and fifth plicae oblique; in most cases these plicae are slightly depressed V-shaped; last plica very slender; there can be an additional, vestigial plica between the last two plicae.

Differential diagnosis: Some populations of *Gudeodiscus multispira* resemble to *Sic. invius* and *Sic. mansuyi*, but these species are smaller, have less whorls and have a strong fold in the aperture, connected to the elevated and sharp parietal callus. *G. yunnanensis*, which is probably the closest relative, has a more elevated spire, is glossier, possesses a smaller aperture and the apertural lip is less developed. Some populations of *G. multispira* (e.g. from Yueling Shan) however are very similar to *G. yunnanensis* (although having more whorls), but the differences between the lamellae and plicae of the two species remain constant. *Gudeodiscus yunnanensis* has only a small plica below (anteriorly to the vertical lamella) and the plicae on the palatal wall are much shorter, often linked together by a ridge. The outer shell characters of the Vietnamese *G. tenuis* resemble those of *G. multispira*, but *G. tenuis* has two lamellae on the parietal wall while its palatal plicae are more oblique and fewer whorls are present. *G. soosi* possesses a flatter shell, stronger sculpture on the dorsal surface, its palatal plicae are connected by a ridge and the parietal denticles are arranged in descending anterior line.

Measurements (in mm): D= 9.4–14.6, H= 4.2–7.7 (n=5, shells from different localities).

Characters of the genital structure: Three specimens were anatomically examined from the following sample: Guangxi, Guilin Shi, Lipu Xian, southern part of Lipu, 190 m, 24°28.909'N, 110°24.024'E, leg. Hunyadi, A., 14.10.2009.

The right ommatophoral retractor crosses the male and female genitalia. Penis cylindrical with a slender proximal and a thicker distal portion; the two portions are about the same size; inner wall of penis densely ribbed; the 22–26 shallow ribs becoming more prominent towards the epiphallus, where the structure is continuous; no hooks found in the penis lumen; same structure also recognisable in the penial caecum; penis 1.4–1.8 times longer than the epiphallus, and 2–2.6 times longer than the penial caecum; long and slender retractor muscle attaches to the penial caecum. Basis of the vagina with a swelling (vaginal bulb), without any remarkable inner structure; vagina tapers towards the end. Vagina with several muscle fibres on one side; gametolytic sac very slender.

All three dissected specimens revealed several (15–19) eggs inside the uterus. The eggs contained well-developed embryos with soft (not calcified) shells. On one side of the egg several calcareous granules could be found.

I also dissected two specimens from a nearby locality (20041112E Guangxi, Qingshan, Qingshan Zhen, Lipu Xian, 252 m, 24°26.189'N, E110°20.008'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 12.11.2004.). The only notable difference is the much shorter penial caecum in the newly examined specimen in relation to the others from the southern part of Lipu.

Radula: Figure 7.101 and Table 7.4.

Distribution: The species was described from "Southern Hunan or Northern Guangdong". I have examined material with exact locality data from Southern Hunan and north-eastern Guangxi (Figure 7.111).

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

Figures 7.13, 7.14, 7.33, 7.42, 7.43, 7.49, 7.67–7.69, 7.91, 7.101

- 1887a *Helix phlyaria* Mabille, Molluscorum Tonkinorum diagnoses: 6 (May).
1887b *Plectopylis phlyaria*, — Mabille, Bulletins de le Société Malacologique de France, 4: 100, pl. 2, Figs 1–3 (July).
1893 *Plectopylis phlyaria*, — Pilsbry, Manual of Conchology..., 2 (8): 158, pl. 43, Figs 40–42.
1896c *Plectopylis phlyaria*, — Gude, Science Gossip, 3: 156.
1897j *Plectopylis phlyaria*, — Gude, Science Gossip, 4: 139, Figs 61a–b. ["Tonkin"].
1899e *Plectopylis (Endoplon) phlyaria*, — Gude, Science Gossip, 4: 148.
1899f *Plectopylis (Endoplon) phlyaria*, — Gude, Science Gossip, 6: 175.
1901b *Plectopylis (Endoplon) phlyaria*, — Gude, Journal of Malacology, 8: 113, Figs 3a–f.
1901b *Plectopylis (Endoplon) moellendorffi* Gude, Journal of Malacology, 8: 115. Figs 4a–f. [Than-Moi] nov. syn.
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 wernerii* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 13: Figs 32, 28–29, 34: Figs 76a–d.
2015 *Gudeodiscus (Gudeodiscus) phlyarius*, — Páll-Gergely et al., Zookeys 472: 41, Figs 4A–F, 5A–C, 9C–D, 10C–F, 11K–X, 12A–M, 21–22, 28A, 28C, 31C, 35J–L.

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

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. Messenger, MNHN-IM-2012-2130/1; Pakhé, leg. Messenger, MNHN-IM-2012-2132/19; Pakhé, leg. Messenger, MNHN-IM-2012-2135/6; Muong-Kong, leg. Messenger, MNHN-IM-2012-2138/2; Muong-Kong, leg. Messenger, MNHN-IM-2012-2140/3; Muong-Hum, leg. Messenger, MNHN-IM-2012-2144/1; Ban-Lao, leg. Messenger, MNHN-IM-2012-2146/28; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2147/29; Pakhé, leg. Messenger, MNHN-IM-2012-2148/3 ("var. *major*"); Pac-Kha (Pakhé), leg. Messenger, MNHN-IM-2012-2155/6 ("var. *major*"); Pac-Kha, leg. Messenger, MNHN-IM-2012-2208/3 ("var. *major*"); Ban-Lao, leg. Messenger, MNHN-IM-2012-2150/22; Pac-Kha (Pakhé), leg. Messenger, MNHN-IM-2012-2157/19; Muong-Kong, leg. Messenger, MNHN-IM-2012-2158/10; Pac-Kha (Pakhé), leg. Messenger, MNHN-IM-2012-2160/22; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2161/28; Pac-Kha (Pakhé), leg. Messenger, MNHN-IM-2012-2168/14; Muong-Kong, leg. Messenger, MNHN-IM-2012-2169/10; Muong-Hum, leg. Messenger, MNHN-IM-2012-2174/1; Muong-Bo, leg. Messenger, MNHN-IM-2012-2178/8; Pac-Kha, leg. Messenger, MNHN-IM-2012-2180/4; Tonkin, leg. Messenger, MNHN-IM-2012-2182/20; Muong-Hum, leg. Messenger, MNHN-IM-2012-2190/7; Long-Ping, leg. Messenger, MNHN-IM-2012-2192/11; Long-Ping, leg. Messenger, MNHN-IM-2012-2206/16; Pac-Kha, leg. Messenger, MNHN-IM-2012-2209/4; Pac-Kha, leg. Messenger, MNHN-IM-2012-2210/2; Muong-Kong, leg. Messenger, MNHN-IM-2012-2244/1; Pakhé, leg. Messenger, MNHN-IM-2012-2245/9; Cao-Bang, leg. Messenger, MNHN-IM-2012-2470/2; Na-Ri, leg. Messenger, MNHN-IM-2012-2463/1; Col de Nuages, leg. Messenger, MNHN-IM-2012-2451/6; Tonkin, leg. Messenger, MNHN-IM-2012-2450/15; Nat-Son, leg. Messenger, MNHN-IM-2012-2445/1; Tonkin, leg. Messenger, MNHN-IM-2012-2442/2; Bac-Kan, leg. Messenger, MNHN-IM-2012-2247/1; Nga-Son, leg. Messenger, 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. Messenger, MNHN-IM-2012-2340/12; Tonkin, leg. Messenger, MNHN-IM-2012-2395/2; Tonkin, leg. Messenger, 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 Messenger, 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 Messenger, NHMW 92565/1; Tonkin, Pac-Kha, NHMW 46226/1; Tonkin, Long-Po (?), coll. Oberwimmer ex Wagner ex Messenger, NHMW 92579/1; Tonkin, Muong-Bo, NHMW 46291/2.

gouldingi/anterides-like shells: Pakhé, leg. Messenger, MNHN-IM-2012-2133/53; Muong-Kong, leg. Messenger, MNHN-IM-2012-2141/14; Na-Ri, leg. Messenger, MNHN-IM-2012-2152/8; Nat-Son, leg. Messenger, MNHN-IM-2012-2153/118; Pac-Kha (Pakhé), leg. Messenger, MNHN-IM-2012-2156/4; Pac-Kha (Pakhé), leg. Messenger, MNHN-IM-2012-2164/44; Bac-Kan, leg. Messenger, MNHN-IM-2012-2167/29; Muong-Kong, leg. Messenger, MNHN-IM-2012-2170/1; Tonkin, leg. Messenger, MNHN-IM-2012-2175/8; Tonkin, leg. Messenger, MNHN-IM-2012-2176/10; Muong-Bo, leg. Messenger, MNHN-IM-2012-2179/1; Nac-Ri, leg. Messenger, MNHN-IM-2012-2187/6; Muong-Hum, leg. Messenger, MNHN-IM-2012-2189/1; Long-Ping, leg. Messenger, MNHN-IM-2012-2193/1; Bac-Kan, leg. Messenger, MNHN-IM-2012-2195/18; Long-Ping, leg. Messenger, MNHN-IM-2012-2197/4; Pac-Kha, leg. Messenger, MNHN-IM-2012-2200/32; Pac-Kha, leg. Messenger, MNHN-IM-2012-2201/15; Tonkin, leg. Messenger, MNHN-IM-2012-2203/1; Long-Ping, leg. Messenger, MNHN-IM-2012-2207/4; Long-Ping, leg. Messenger, MNHN-IM-2012-2213/2; Cho-Ra, leg. Messenger, MNHN-IM-2012-2478/1; Bac-Kan, leg. Messenger, MNHN-IM-2012-2476/2; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2473/6; Bac-Kan, leg. Messenger, MNHN-IM-2012-2465/4; Na-Ri, leg. Messenger, MNHN-IM-2012-2464/1; Na-Ri, leg. Messenger, MNHN-IM-2012-2462/8; Tonkin, leg. Messenger, MNHN-IM-2012-2459/1; Pakhé, leg. Messenger, MNHN-IM-2012-2454/8; Col de Nuages, leg. Messenger, MNHN-IM-2012-2452/15; Nat-Son, leg. Messenger, MNHN-IM-2012-2446/1; Col de Nuages, leg. Messenger, MNHN-IM-2012-2214/9; Na-Ri, leg. Messenger, MNHN-IM-2012-2220/8; Pakhé, leg. Messenger, MNHN-IM-2012-2226/5; Tonkin, leg. Messenger, MNHN-IM-2012-2228/1; Muang-Kong, leg. Messenger, MNHN-IM-2012-2243/7; Nat-Son, leg. Messenger, MNHN-IM-2012-2256/12; Phi-Mi, leg. Messenger, MNHN-IM-2012-2334/1; Tonkin, leg. Messenger, MNHN-IM-2012-2372/3; Muong-Kong, leg. Messenger, MNHN-IM-2012-2429/8; Bac-Kan, leg. Messenger, MNHN-IM-2012-2433/16; Bac-Kan, leg. Messenger, MNHN-IM-2012-2436/1; Tonkin, leg. Messenger, MNHN-IM-2012-2422/8; Pakhé, leg. Messenger, MNHN-IM-2012-2389/2; Bac-Kan, leg. Messenger, 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. Messenger, MNHN-IM-2012-2438/1; Tonkin, leg. Messenger, 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 Messenger, NHMW 71640/O/9478/2; Tonkin, Bac-Kha, coll. Rušnov ex Rolle ex Messenger, NHMW 92566/2; Tonkin, Pac-Kha, NHMW 46225/2; Tonkin, Pac-Kha, coll. Wagner ex Messenger, NHMW 71640/O/10290/1; Tonkin, Long-Phai, coll. Wagner ex Messenger, NHMW 71640/O/10291/1; Tonkin, Pac-Kha, NHMW 92568/1; Tonkin, Pac-Kha, NHMW 46292/2; Tonkin, Bac-Kan, coll. Wagner ex Messenger, NHMW 71640/O/10292/1; Tonkin, Bac-Kan, coll. Oberwimmer, NHMW 71640/O/14029/3; Tonkin, Nat-Son, coll. Rušnov ex Messenger, NHMW 103354/1.

"Mixed" *gouldingi/anterides/fallax* samples: Bac-Kan, leg. Messenger, MNHN-IM-2012-2171/20; Trinh-Thuong, leg. Messenger, MNHN-IM-2012-2181/44; Pakhé, leg. Messenger, MNHN-IM-2012-2185/31; Muong-Bo, leg. Messenger, MNHN-IM-2012-2211/3; Col de Nuages, leg. Messenger, MNHN-IM-2012-2218/25; Col de Nuages, leg. Messenger, MNHN-IM-2012-2222/15; Tonkin, leg. Messenger, MNHN-IM-2012-2224/13; Tonkin, Pac-Kha, coll. Dosch ex Rolle ex Messenger, 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. Messenger, MNHN-IM-2012-2212/5; Long-Phai, leg. Messenger, 1901, MNHN-IM-2012-2232/1; Than-Moi, coll. Staat, 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. Messenger, MNHN-IM-2012-2474/1; Tonkin, leg. Messenger, MNHN-IM-2012-2427/3; Tonkin, leg. Messenger, MNHN-IM-2012-2431/1; Tonkin, leg. Messenger, MNHN-IM-2012-2391/1; Bac-Kan, coll. Staat, 1969, MNHN-IM-2012-2392/2; Than-Moi, coll. Staat, 1969, MNHN-IM-2012-2397/5; Than-Moi, coll. Staat, 1969, MNHN-IM-2012-2398/1; Lang-Son, coll. Letellier, 1949, MNHN-IM-2012-2401/1; Than-Moi, coll. Staat, 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 Messenger, 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. Messenger, MNHN-IM-2012-2177/9; Nat-Son, leg. Messenger, MNHN-IM-2012-2447/6; Phong-Tho, leg. Messenger, MNHN-IM-2012-2443/4; Phong-Tho, leg. Messenger, 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 Ngâm 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., 04.10.2011., HE/21 (+2 specimens in ethanol, one of them anatomically examined); 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.

phlyariis-like, mainly flat, small form:

China, Guangxi, Bose Shi, Lingyun Xian, Xiajia Xiang, SE part of Xiajia, rocky wall above the graves, 440 m, 24°17.508'N, 106°38.376'E, leg. Hunyadi, A., 22.10.2009, HA/4, PGB/1; China, Guangxi Guangxi, Dahuayaozu Zizhixian, Jiangnan Xiang, near bus stop at crossroad in Liupeng, 206 m, 23°55.576'N, 107°38.903'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 23.10.2011, OK/1, PGB/2; China, Guangxi Guangxi, Dahuayaozu Zizhixian, Liming Xiang, Hongjunyan, 255 m, 23°48.374'N, 107°31.455'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 23.10.2011, OK/3, PGB/1; China, Guangxi Guangxi, Laibin Shi, Qidong Xiang, Ganchaoyan, 168 m, 24°00.791'N, 109°04.372'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 25.10.2011, OK/1; **Vn10-53** Vietnam, Lang Son Province, right off rd. 1B Long Đông to Bình Giả, 21°53.938'N, 106°25.605'E, leg. Hemmen, Ch. & J., 20.3.2010., PGB/3; **Vn10-48** Vietnam, 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** Vietnam, 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** Vietnam, 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** Vietnam, 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** Vietnam, 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** Vietnam, 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** Vietnam, Lạng Sơn Province, ca. 7 km from Đồng Mô 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** Vietnam, 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** Vietnam, 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** Vietnam, 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 Giả to Lạng Sơn on road 1B (no GPS data), leg. Hemmen, Ch. & J., 01.04.2011., HE/11; **Vn11-156** Vietnam, Lạng Sơn

Province, ca. 10.6 km from Binh 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); **Vn11-157** Vietnam, Lạng Sơn Province, ca. km. 50 of road 1B, 10 km to Binh Gia, 21°53.911'N, 106°25.664'E, leg. Hemmen, Ch. & J., 01.04.2011., HE/6 (in ethanol); **2011/65** Vietnam, Lạng Sơn Province, Đồng Mô 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** Vietnam, Lạng Sơn Province, Đồng Mô 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** Vietnam, Lạng Sơn Province, Đồng Mô 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** Vietnam, Lạng Sơn Province, Đồng Mô 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** Vietnam, Lạng Sơn Province, Lạng Sơn, NNE side of Núi Vong Phu, 21°51.183'N, 106°44.950'E, leg. Hunyadi, A., 11.11.2011., HA/3; **2011/72** Vietnam, 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** Vietnam, 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** Vietnam, 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** Vietnam, 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** Vietnam, 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** Vietnam, Lạng Sơn Province, Đồng Mô 7 km towards Chi Lăng, right side of the road, leg. Hunyadi, A., 13.11.2011., HA/1; **2011/79** Vietnam, Lạng Sơn Province, Đồng Mô 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** Vietnam, Lạng Sơn Province, Đồng Mô 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** Vietnam, Lạng Sơn Province, Đồng Mô 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** Vietnam, 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., 02.04.2011., HE/1; **Vn11-158** Vietnam, Lạng Sơn Province, ca. 7.5 km foad 1B from Binh Gia to Bắc Sơn, 21°53.908'N, 106°25.661'E, leg. Hemmen, Ch., 01.04.2011., HE/1; **Vn09-06** Vietnam, Ninh Bình Prov., Cúc Phương N. P., 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; **VERM2** Vietnam, 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 7.119); **MAA10** Vietnam, 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. (3 specimens) (marked with no. 3 on Figure 7.119); **Vn10-41** Vietnam, 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 7.119).

larger, strongly built shell. (transition to *wernerii*): China, Guangxi, Nanning Shi, Longan Xian, Longhushan Senlin Gongyuan, 600 m from the entrance, Peri Hill, leg. Hunyadi, A., 11.10.2009, HA/17; **2009/82** China, Guangxi, Nanning Shi, Longan Xian, Longhushan Senlin Gongyuan, Peri Hill, 140 m, 22°57.485'N, 107°37.754'E, leg. Hunyadi, A., 11.10.2009, HA/25, PGB/5; China, Guangxi, Hechi City, ex coll. YangHao, 2011, PGB/6; Guangxi, Heshan Shi, Beisi Xiang, Baxiyanan, 120 m, 23°49.510'N, 108°55.942'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 14.11.2004, OK/14, PGB/5; China, Guangxi, Pingguo Xian, Duiwei Xiang, Guiyan, 102 m, 23°41.580'N, 107°49.879'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 23.10.2011, OK/3, PGB/1; China, Guangxi, Duanyaozu Zizhixian, Baoan Xiang, Yuanli, 616 m, 24°06.313'N, 107°50.216'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 22.10.2011, OK/1; China, Guangxi, Dahuayaozu Zizhixian, Prefectural border at Qibainong Xiang, 688 m, 24°06.496'N, 107°41.466'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 22.10.2011, OK/1; China, Guangxi, Duanyaozu Zizhixian, Baoan Xiang, Nongjiao, 607 m, 24°05.580'N, 107°46.971'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 24.10.2011, OK/4, PGB/3; China, Guangxi, Dahuayaozu Zizhixian, Guhe Xiang, Xiannudong, 212 m, 23°54.321'N, 107°44.566'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 23.10.2011, SMF 341512/1, OK/10, PGB/5; China, Guangxi, Dahuayaozu Zizhixian, Qibainong Xiang, near bus stop at Nongteng, 603 m, 24°04.905'N, 107°41.100'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 22.10.2011, OK/1; China, Guangxi, Dahuayaozu Zizhixian, near Guhe Xiang, 215 m, 23°54.456'N, 107°44.101'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 23.10.2011, OK/1, PGB/1.

wernerii-like shells: Guangxi, Hechi Shi, Duan Yaozu Zizhixian, Gaoling Cun, Dingfu Cun W 2 km, 320 m, 24°03.197'N, 108°01.290'E, leg. Hunyadi, A., 8.10.2009, holotype HNHM 97438, paratypes HA/7, PGB/2; Guangxi,

Duanyaozu Zizhixian, Baoan Xiang, Nongyao, 340 m, 24°04.338'N, 107°55.597'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 24.10.2011, OK/4, PGB/4; Guangxi, collected by local collectors, ex coll. He Jing, PGB/7; Guangxi, Duan, leg. Zhao Yifan, 2005 (35 dextral, 1 sinistral shell), EZP/2, NHMW 108168/2, SMF 341513/2, NHMUK 20120001/1, PGB/26+1; Guangxi, Duan, leg. Zhao Yifan, 2005 Dec., JG/2, Guangxi, ex coll. Zhao Yifan, EZP/7, JG/2.

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.

Description of typical *phlyarius*: Shell flat or depressed-conical, brownish, yellow or corneous; whorls 7–7.5, suture rather shallow; teleoconch very finely ribbed, and the ribs are spirally decussate; sculpture is weaker, but also recognisable on the ventral surface; umbilicus moderately wide and deep; apertural margin moderately thickened, however, this character varies greatly within populations; a short apertural fold is usually present, missing on exception; positioned free from the callus.

More than ten specimens were opened from Vietnamese and Chinese populations. Parietal wall with two vertical lamellae and two horizontal plicae above and below; plicae primarily free however in older specimens, the ends of the anterior lamella can be fused with the plicae; the palatal wall with six plicae; first slender, running parallel with the suture; last very short and curved; remaining ones usually connected by a ridge.

Intraspecific diversity: Extremely large. Table 7.7 summarizes the conchological differences between newly collected Vietnamese *G. phlyarius* samples.

Differential diagnosis: In China *G. phlyarius* can be distinguished from *G. giardi* by the flatter shell, wider umbilicus and the relatively free plicae on the parietal wall. *G. yanghaoi* is ventrally smooth, has a thicker apertural rim and a long apertural fold, sometimes connected to the callus. Additionally, the palatal plicae of *G. yanghaoi* are prominently connected to each other and form a strong vertical plica. *G. eroessi*, *G. okubo* and *G. pulvinaris* have only a single lamella on the parietal wall. See also under *Gudeodiscus anceyi*, *G. emigrans*, *G. giardi*, *G. hemmeni* u. sp., *G. messengeri* and *Halongella fruhstorferi*.

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). The size range is continuous to from typical *anterides* to *fallax* var. *major*; 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); D= 17.4–19.3, H= 8.0–9.3 (n=4, "*wernerii*").

Characters of the genital structure:

typical *fallax*: Two specimens were anatomically examined (Lào Cai Province, ca. 3 km SW of Nhà Văn Hóa, 22°25.513'N, 104°12.194'E, leg. Hemmen, Ch., 04.10.2011).

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 arranged 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 Binh Gia to Lạng Sơn on road 1B, 21°53.639'N, 106°25.895'E, leg. Hemmen, Ch. & J., 01.04.2011.; Lạng Sơn Province, ca. km. 50 of road 1B, 10 km to Binh Gia, 21°53.911'N, 106°25.664'E, leg. Hemmen, Ch. & J., 01.04.2011.

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; the distal part of the vagina is strongly folded; gametolytic sac and diverticulum of equal length, both being relatively short. **Chinese *phlyarius*:** Three specimens were dissected: "*phlyarius1*" (without developing eggs in the uterus: Longhushan Senlin Gongyuan, 600 m from the entrance); "*phlyarius2*": (with 26 embryos in the uterus: Guiyan); "*phlyarius3*" (with 4 embryos in the uterus: Xiannudong). The right ommatophoral retractor crosses the genitalia; penis long or middle-sized; in "*phlyarius1*" comprised of a longer proximal and a shorter club-like distal portion, in "*phlyarius3*" no separation was detectable. Inner penis wall with low, parallel ribs, which gradually become stronger towards the distal end; before the margin of the proximal and distal ends, pockets are formed by parallel folds on the inner surface. In "*phlyarius1*", twenty-one (probably stimulatory) hooks (0.4–1.8 mm in height) were found between the top sections of the folds lining the inner penis wall. The low parallel structure is also recognisable in the penial caecum and the epiphallus. In *phlyarius1* and *phlyarius2* the penis is about three times, in *phlyarius3* only slightly longer than the epiphallus. Vas deferens very long; vagina also long with a swelling (vaginal bulb) at the base.

Radula: Figure 7.101 and Table 7.4.

Distribution: The populations assigned to *G. phlyarius* inhabit several regions of Northern Vietnam (Lang Son, Cao Bang, Ninh Binh, and along the border region with the Chinese Yunnan Province) and the Chinese Guangxi (Figure 7.119).

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*, *messengeri*, *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 weak peristome and callus. Therefore, it is discussed separately, under the name *Gudeodiscus cyrtochilus*. In face of the obvious similarities between the remaining five species, *Plectopylis messengeri* and *P. fallax* were only compared with *P. moellendorffi*, and *P. verecunda* was compared with *P. messengeri*. 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 *messengeri* 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. messengeri* and the sympatric species referable to *fallax*, *gouldingi* and *anterides* are stable, therefore *Gudeodiscus messengeri* is handled separately from the rest of the taxa.

I have investigated several samples of flat *G. phlyarius* (similar to the type specimens deposited in the MNHN) from Vietnam (mainly from Lang Son Province). Still, some shells have an elevated spire, resembling Gude's (1901) *moellendorffi* (Tonkin, Than-moi, coll. Möllendorff, ex Fruhstorfer, lectotype, SMF 150125a). Since no geographical patterns and other distinguishing shell characters were found, I have to synonymize *moellendorffi* with *phlyarius*.

In our revision of the Chinese members of the family (Páll-Gergely & Hunyadi 2013), *G. phlyarius* was reported from several localities in Guangxi. *G. phlyarius wernerii* was described from two nearby localities near Duan city. All other Chinese *G. phlyarius* populations were assigned to the nominotypical subspecies. *G. 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 *wernerii*)".

Here I 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, *wernerii* 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 *Gudeodiscus phlyarius* is a widely distributed, very variable species and at this moment I see no good reason to maintain one of the morphologically distinct form as a subspecies. Consequently, I synonymize *G. phlyarius wernerii* 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. Messenger, MNHN-IM-2012-2153, containing 118 "*gouldingi*" shells). The length of the lower

horizontal plica varies greatly, but exceeds the anterior lamella anteriorly 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 Messenger. Examining the Type material 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 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 Messenger'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. On the other hand, I 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 (see Figure 7.132).

The apertural fold is always present on typical *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). 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. Even this difference is found to be variable in Chinese populations. The populations listed as "transitions to *wernerii*" in Páll-Gergely & 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, I refer to *anterides*, *gouldingi* and *fallax* as synonyms of *Gudeodiscus 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 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. *G. multispira*). 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 *G. phlyarius*. Seven of the shells were typical *verecundus* with elevated spire, strong apertural fold connected to the callus and the anterior lamella was fused to the lower plica; the plica 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 was 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, I synonymise *Plectopylis verecunda* with *Gudeodiscus phlyarius*.

There are two Vietnamese "forms" of *G. phlyarius* which differ from all other typical Vietnamese *phlyarius* shells. One of the morphologically distinct forms inhabits Ninh Binh Province, where I have knowledge of two populations (number 3 on Figure 7.119). These shells are smaller and comparatively flatter than the usual *phlyarius*, and have 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 7.119). 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 exceed the lamella.

Two Chinese populations (near Baxianyan, number 1 on Figure 7.119) have an oblique anterior lamella and an aperture more reflected downwards.

***Gudeodiscus (Gudeodiscus?) soosi* Páll-Gergely 2013**

Figures 7.10, 7.47

2013 *Gudeodiscus soosi* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 31, Figs 42a–b, 66.

2015 *Gudeodiscus (Gudeodiscus?) soosi*, — Páll-Gergely et al., Zookeys 472: 14.

Type material: Guangxi, Tiane Xian, Qimu Xiang, Lahaoyan, 685 m, 24°50.993'N, 107°09.963'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 21.10.2011, holotype HNHM 97482, paratypes SMF 341515/1, HA/1, OK/5, PGB/3; Guangxi, Tiane Xian, Qimu Xiang, Duloulieshita, 602 m, 24°51.114'N, 107°11.666'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 21.10.2011, OK/1; Guangxi, Tiane Xian, Liupai Zhen, Shuiliandong, 354 m, 25°00.623'N, 107°09.994'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 21.10.2011, HNHM 97483/1, OK/5, PGB/3.

Diagnosis: A small, almost flat species with thin, translucent shell, finely ribbed dorsal surface and a small denticle in the aperture. Parietal wall with one lamella and five well-developed plicae and denticles anteriorly; a ridge connects the short horizontal palatal plicae.

Description: Shell depressed, almost flat, yellowish-corneous or light brown, thin-walled, translucent; whorls 6.5–7, separated by rather deep suture; dorsal surface of the teleoconch irregularly wrinkled, radial lines most conspicuous near the suture; umbilicus moderately wide; aperture with slightly protruded upper sinus; apertural margin only slightly thickened and reflected; one short, low fold is free from the weak callus.

Five specimens were opened from different locations. Parietal wall with one lamella and two long horizontal plicae anteriorly, one above and one below; upper one much longer. Between these plicae there are three well-developed denticles, the uppermost is the closest to the lamella. Sometimes the denticles are slightly connected with a ridge. Palatal plicae six in number, short, parallel and horizontal, always connected with a ridge.

Differential diagnosis: *Gudeodiscus soosi* flatter than *G. multispira*, has relatively larger aperture and has connected palatal plicae; the parietal denticles between the horizontal plicae are stronger. The uppermost denticle is situated most posteriorly, whereas the lowest is found closest to the aperture. *G. yunnanensis* has a more elevated spire; the apertural fold is missing and has a lamella with only one denticle in front on the parietal wall.

Measurements (in mm): D= 9.9–12.5, H= 4.2–5.3 (n=3).

Etymology: *Gudeodiscus soosi* is dedicated to the prominent Hungarian malacologist, Lajos Soós (1879–1972) to commemorate the fortieth anniversary of his death.

Type locality: Guangxi, Tiane Xian, Qimu Xiang, Lahaoyan, 685 m, 24°50.993'N, 107°09.963'E.

Distribution: *Gudeodiscus soosi* is known from two nearby locations in Northern Guangxi (Figure 7.113).

Remarks: The population from Shuiliandong is much flatter and has slightly stronger sculpture.

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

Figures 7.8, 7.45

1908b *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 Molluskenkunde 142 (1): 8.

2015 *Gudeodiscus (Gudeodiscus?) suprafilaris*, — Páll-Gergely et al., Zookeys 472: 54, Figs 9A–B, 9R, 14S–Y.

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

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

New material examined: Vn10-125 Cao Bằng Province, ca 60 km from Cao Bằng to Báo 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; **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 Ráo, 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. 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.

Differential diagnosis: The shells shape of *G. suprafilaris* is similar to that of *G. infralevis*, but *G. suprafilaris* has more regular whorls, 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* Páll-Gergely & Hunyadi 2013 which have similar sculpture are larger, have a flatter shell and different lamellation.

Measurements (in mm): D= 13.1, H= 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).

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 7.8.

Distribution: Examined material was from only Cao Bằng and Lạng Sơn Provinces. The type locality (Quang-Huyen) lies in Cao Bằng Province (Figure 7.116).

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 possesses a well-developed posterior lamella, upper and lower plica, and a reduced, short anterior lamella. The museum specimens I 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 and 2012/44) were examined. Shells belonging to both populations had very similar 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) the horizontal plicae on the vertical plica 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?) ursula Páll-Gergely & Hunyadi 2013

Figures 7.17, 7.44

2013 *Gudeodiscus ursula* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 32, Figs 16, 52a–d.

2015 *Gudeodiscus (Gudeodiscus?) ursula*, — Páll-Gergely et al., Zookeys 472: 14.

Type material: China, Guangxi, Pinguo county, ex coll. Zhao Yifan, holotype HNHM 97454, paratypes NHMW 108170/1, NHMUK 20120003/1, SMF 341516/1, EZP/1, HUA/2, JG/1, PGB/4.

Diagnosis: A small, white species with irregularly increasing whorls. Parietal wall with a vertical lamella and two horizontal plicae anteriorly near the sutures; between these two plicae there are five horizontal plicae.

Description: Shell depressed; spire only slightly elevated; white or off-white; aperture yellowish; first 1–1.5 whorls of the protoconch smooth; the approximate remaining one whorl very finely, regularly ribbed; teleoconch very finely wrinkled; whorls 6–6.5; irregularly increasing and separated by rather deep suture; umbilicus very wide; apertural rim slightly thickened and reflected; some specimens (probably shells of more mature specimens) have elevated parietal callus, which is relatively sharp; a small denticle may be present in the aperture, never reaching the callus.

Three specimens were opened. Parietal wall with two longer plicae above and below, near the suture; between these plicae five additional shorter plicae which are thicker near the lamella, tapering anteriorly; palatal wall with five plicae, connected by a callous ridge, first is the longest; there is always a small, short additional plica near the posterior ends between the two last plicae.

Differential diagnosis: This species demonstrates very unique conchological features (small, white shell with several horizontal lamellae on the parietal wall). Hence, it can be easily distinguished from other Plectopylidae species. The parietal wall of *G. ursula* possesses seven horizontal plicae. In the case of some other Plectopylidae species (e.g. *S. reserata*, *S. stenochila*, *S. murata*, *G. multispira*, *S. asamiana*, *G. phlyarius wernerii*), there are only 2–3 short denticles between the horizontal plicae (4–5 plicae altogether) anterior of the single vertical lamella. *G. emigrans* and *S. reserata hensanensis* possesses four long horizontal plicae in front of the lamella. The Vietnamese *Gudeodiscus emigrans quadrilamellatus* (and seldom *G. emigrans otanii*) has four long horizontal plicae on the parietal wall. These taxa however are bigger, darker and have a different shell shape.

Measurements (in mm): D= 9.3–10.0 H= 4.5–4.6 (n=5).

Etmology: The vertical lamella and the horizontal plicae on the parietal wall resemble a bear claw. The name "ursula" (used as noun, gender female) is the diminutive form of the Latin ursus (bear).

Type locality: China, Guangxi, Pinguo County.

Distribution: The species is known from the type locality only (Figure 7.118).

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

Figures 7.6, 7.31, 7.44, 7.70–7.71, 7.91, 7.94, 7.102

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

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

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

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

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

1900a *Plectopylis Villedaryi* Gude, The Annals and magazine of natural history 7 (5): 313.

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

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

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

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.

2015 *Gudeodiscus (Gudeodiscus) villedaryi*, — Páll-Gergely et al., Zookeys 472: 56, Figs 8B–D, 9J, 10B, 13V–Y, 23–24, 28F–G, 30A–C, 30F, 32D, 35M–O.

Types examined: Haut-Tonkin, NHMUK 1930.9.12.38 (holotype of *villedaryi*); Tonking, Than-Moi, collection Möllendorff ex Fruhstorfer, SMF 9279 (lectotype of *choanomphala*); 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, HNHN 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 Thà, 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 Messenger, NHMW 92586/2; Tonkin, Than Moi, coll. Edlauer ex Rolle, NHMW 75000/E/7816/3; Tonkin, Nja-Ba-Thà (?), coll. Rušnov ex Blume, NHMW 92584/1; Tonkin, Than-Moi, coll. Rušnov ex Rolle ex Messenger, 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, Phương Hoàng Cave, 21°46.554'N, 106°07.210'E, leg. Hemmen, Ch. & J., 18.03.2010., PGB/3; **20090520A** Thái Nguyên Province, Võ Nhại District, Phú Thượng Commune, Phương Hoàng Cave, Mỏ Gà Vill., 146 m, 21°46.836'N, 106°07.107'E, leg. Ohara, K., 20.05.2009., OK/15, PGB/4; **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 Mô 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 Mô 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 Mô 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, Phụng 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); **2012/38** Lạng Sơn Province, Đồng Mô 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., 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., 02.04.2011., HE/9; **Vn11-151** Thái Nguyên Province, ca. 48 km from Thái Nguyên to Bắc Sơn, near Lâu Thượng (SW Đình Cả), 21°43.522'N, 105°58.662'E, leg. Hemmen, Ch., 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; 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.

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

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, 2009.05.20A); 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).

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 7.9.

Characters of the genital structure: 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 about 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; there is a shorter, thicker gametolytic sac and a longer, more slender diverticulum.

Radula: Figure 7.102 and Table 7.4.

Distribution: The species is known from Thái Nguyên and Lạng Sơn provinces (Figure 7.115).

Remarks: *G. villedaryi* is a very variable species in terms of shells characters. I recognise the species 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 a monophyletic group. See also under *Gudeodiscus dautzenbergi*.

The two hypothesis which explains the origin of the lower parietal plica are explained in Chapter 8 (Assumption 11, Figures 8.29 and 8.30).

***Gudeodiscus (Gudeodiscus?) yanghaoi* Páll-Gergely & Hunyadi 2013**

Figures 7.17, 7.44

2013 *Gudeodiscus yanghaoi* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 32, Figs 57a–b, 67.

2015 *Gudeodiscus (Gudeodiscus?) yanghaoi*, — Páll-Gergely et al., Zookeys 472:14.

Type material: Guangxi, Baise (Bose) Shi, ex coll. YangHao, holotype HNHM 97441, paratypes EZP/1, HA/1, PGB/1.

Diagnosis: A middle-sized to large, brownish *Gudeodiscus* species with remarkably thickened apertural lip. Excepting the first, all of the palatal plicae are connected and can be seen as a continuous single vertical lamella; parietal wall with two vertical lamellae and two horizontal plicae.

Description: Shell flat-conical; brownish corneous; consists of 6.25–7.25 flat whorls; teleoconch very finely ribbed, with weaker spiral lines; the smooth and ribbed surface structure changes abruptly at about mid body whorl; umbilicus extremely wide; aperture relatively narrow in relation to shell width; apertural lip light brown/cream coloured; very well-developed; thick and slightly reflected; parietal callus elevated, sharp; at the junction of the parietal callus and the lip with two shallow canals on both sides, therefore the two rims are not in contact; aperture with a slender, relatively long fold, weakly connected to the callus.

Two specimens were opened. Parietal wall with two vertical lamellae; anterior more or less straight with upper and lower part widened; posterior lamella more curved; with upper and lower branches elongated posteriorly; short horizontal plica is visible above the anterior lamella (not in contact with it); and a longer plica runs parallel with the lower suture; it joins with the posterior lamella; palatal wall with about 5 plicae, first slender and horizontal, last slightly thicker and shorter; middle plicae form a continuous line, which looks like a vertical "lamella" when viewed from the outside in; it is almost impossible to determine how many plicae join together.

Differential diagnosis: *Gudeodiscus yanghaoi* has a very unique appearance in regards to its relatively small aperture and thick apertural rim as well as its unusual shell colour and sculpture.

Measurements (in mm): D= 18.6–21.3, H= 8.0–9.4 (n=3).

Etymology: This species is named after Yang Hao, the collector and provider of material for our revision.

Type locality: Guangxi, Baise (Bose) Shi.

Distribution: *Gudeodiscus yanghaoi* is known from the type locality only (Figure 7.118).

***Gudeodiscus (Gudeodiscus?) yunnanensis* Páll-Gergely 2013**

Figures 7.10, 7.47

2013 *Gudeodiscus yunnanensis* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 33, Figs 18, 40a–b.

2015 *Gudeodiscus (Gudeodiscus?) yunnanensis*, — Páll-Gergely et al., Zookeys 472:14.

Type material: Yunnan, Guangnan Xian, Wenshan Zhuangzu Miaozu Zizhizhou, Liji, 1611 m, 23°45.54175'N, 104°59.55567'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 13.6.2005, holotype HNHM 97443, paratypes HA/1, OK/13, PGB/1.

Diagnosis: A small, depressed discoid, glossy species with weak apertural lip and callus. Parietal wall with a single lamella.

Description: The outer shell characters are indistinguishable from that of *G. cyrtochilus*. In size it is similar to Chinese *G. cyrtochilus* specimens. *Gudeodiscus yunnanensis* has 6–6.5 whorls.

Two specimens were opened. Parietal wall with a single curved lamella; anterior one totally reduced; sometimes with an additional denticle anteriorly below; palatal wall with six major plicae and an additional plicula between the last and the penultimate plicae near the posterior end of the last plica; first plica vestigial; situated close to the suture; last one also slender; other plicae (second–fifth) of the same length; are straight and are connected by a continuous ridge.

Differential diagnosis: This species is indistinguishable from *G. cyrtochilus* particularly if the parietal lamellae are not examined. *G. cyrtochilus* has two lamellae, whereas *G. yunnanensis* has only one. Some populations of *G. multispira* (e.g. from Yueliang Then) are very similar to *G. yunnanensis*, which has 0.5–1 whorl less, but the differences are visible mainly in the armature. *G. yunnanensis* has short, parallel and horizontal palatal plicae connected by a callous ridge; the plicae of *G. multispira* are depressed Z-shaped, longer and oblique. *G. multispira* usually has some denticles anterior to the curved parietal lamella and an upper horizontal plica is always present. *G. yunnanensis* has reduced parietal lamellation minus remnants of the anterior lamella while the upper horizontal plica is missing.

Measurements (in mm): D= 10.8–11, H= 5.5–5.8 (n=3).

Etymology: This species is named after its occurrence in the Province of Yunnan.

Type locality: Yunnan, Guangnan Xian, Wenshan Zhuangzu Miaozu Zizhizhou, Liji, 1611 m, 23°45.54175'N, 104°59.55567'E.

Distribution: The species is known only from the type locality in southeastern Yunnan (Figure 7.111).

Subgenus *Veludiscus* Páll-Gergely 2015

2015 *Gudeodiscus (Veludiscus)* Páll-Gergely in Páll-Gergely et al., Zookeys 472: 59.

Type species: *Gudeodiscus eroessi* Páll-Gergely, 2013.

Diagnosis: Shell indistinguishable from those of the subgenus *Gudeodiscus (Gudeodiscus)* and the genus *Halongella*. 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.

Differential diagnosis: *Gudeodiscus (Veludiscus)* species differ from *Gudeodiscus (Gudeodiscus)* species by the slender epiphallus, and the muscle fibres which cover the distal part of the penis including the penial caecum. The central tooth is smaller than the ectocone of the first laterals (as large, or larger in *Gudeodiscus*), and the marginals bi- or tricuspid, with blunt inner cusp and shallow incision between the inner two cusps (tricuspid with pointed cusps are deep incision in *Gudeodiscus*).

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 middle-sized to large, flat *Gudeodiscus* species, with dense, fine riblets; callus always, denticles 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 in front of the lamella.

Differential diagnosis: *Gudeodiscus phlyarius* has stronger apertural fold, straight anterior parietal lamella (in the Chinese *G. phlyarius weneri* Páll-Gergely 2013 sometimes dissolved into small denticles) and usually somewhat elevated spire. *G. messengeri*, *G. hemmeni* u. sp. and *G. anceyi* have two parietal lamellae or several small denticles standing in a line at the position of the first lamella. *Gudeodiscus emigrans* has weaker sculpture than *G. okuboi*, and in the latter species the apertural fold is missing. *G. eroessi* is smoother and has weaker callus. *G. concavus* has concave shell with more oblique aperture.

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

Gudeodiscus (Veludiscus) emigrans emigrans (Möllendorff 1901)

Figures 7.12, 7.47

- 1901a *Plectopylis (Sinicola) emigrans* Möllendorff, Nachrichtenblatt 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).
- 2015 *Gudeodiscus (Veludiscus) emigrans emigrans*, — Páll-Gergely et al., Zookeys 472: 60, Figs 6E, 13A–B.

Types examined: Tonkin: Mansen-Gebirge, coll. Möllendorff ex Fruhstorfer, lectotype SMF 9256; Tonkin: Mansen-Gebirge, coll. Möllendorff ex Fruhstorfer, paralectotype SMF 9257.

Museum material examined: Tonkin: Mansongebirge, leg. Fruhstorfer, SMF 150083/1; Tonkin, Montes Mauson, April–May, 2–3000", NHMUK 1901.12.12.209–210/2.

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

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*). Moreover, some specimens of *G. emigrans otanii* have two vertical lamellae.

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

Intraspecific diversity: Very few shells are known from museums collections. The subspecies is easily recognisable, but more material is needed to understand the intraspecific diversity.

Distribution: *Plectopylis (Sinicola) emigrans* was described from the „Manson-Gebirge” = "Mau Son Mts, about 30 km E of Lang Son" (Schileyko, 2011) (Figure 7.110).

***Gudeodiscus (Veludiscus) emigrans otanii* Páll-Gergely 2013**

Figures 7.12, 7.47, 7.72, 7.73, 7.90, 7.96, 7.99

- 2013 *Gudeodiscus emigrans otanii* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 12–15, Figs 25–26, 46a–c, 58 (map).
- 2014a *Gudeodiscus emigrans otanii*, — Páll-Gergely & Asami, Genus 25(3): 529–533, Figs 5F–H, 6–7, 20A–B.
- 2015 *Gudeodiscus (Veludiscus) emigrans otanii*, — Páll-Gergely et al., Zookeys 472:60, Fig. 34A–C, Tables 3, 6.

Type material: Guangxi, Yizhou Shi, Shibie Xiang, Qingtan, 225 m, 24°23.719'N, 108°42.137'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 13.11.2004, holotype HNHM 97446, paratype, PGB/3; **20041113B** Guangxi, Yizhou Shi, Aishan Xiang, Xiannuyan, 172 m, 24°29.292'N, 108°34.057'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 13.11.2004, HA/1, PGB/3; Guangxi, Liuzhou Shi, Yufeng Qu, Longtang Gongyuan, 80 m, 24°16.836'N, 109°24.430'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 13.3.2009, PGB/1; Guangxi, Duanyaozu Zizhixian, Gaoling Zhen, Baheng, 183 m, 24°04.332'N, 108°04.010'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 22.10.2011, OK/1.

Additional material: Guangxi, Laibin Shi, Xingbin Qu, Qidong Xiang, cliffs above the Poliu Elementary School, 150 m, 24°0.512'N, 109°4.288'E, leg. Hunyadi, A. & Szekeres, M., 20.09.2013., HA/12, PGB/2.

Diagnosis: A middle-sized to large, flat *Gudeodiscus* subspecies, with dense riblets. There is an elevated, sharp callus and a small free denticle in the aperture. On the parietal wall, a C-shaped posterior lamella and a slightly S-shaped anterior lamella can be seen. There are two horizontal plicae above and below the anterior plica.

Description: Shell brownish, almost flat, widely umbilicated, with 6.5–6.75 whorls; teleoconch finely, rather irregularly ribbed; sometimes inconspicuous spiral structure between riblets; sculpture weaker on ventral side; riblets lower and spiral structure as strong as the riblets; apertural rim brownish, thickened and slightly reflected; callus elevated, relatively sharp with canals at both ends; a small, white, free denticle usually present in the aperture, but lacking in some specimens.

Six specimens were opened from different localities. Parietal wall with C-shaped posterior lamella and a slightly S-shaped anterior lamella; two horizontal plicae above and below the anterior lamella; palatal wall with six plicae, first and last are simple, straight and relatively weak; second-fifth plicae with depressed Z-shape and are supported by an additional plica posteriorly; some plicae fused with that additional plicula, as a result they demonstrate a Y-like shape.

Differential diagnosis: *Gudeodiscus emigrans otanii* differs from the Vietnamese *G. emigrans quadrilamellatus* by the less prominent spiral structure. *G. emigrans otanii* has two lamellae on the parietal wall; whereas *G. emigrans*

quadrilamellatus usually has four parallel plicae anterior to the lamella (see remarks). *G. emigrans emigrans* (reported also from Vietnam) has only a single denticle anteriorly below of the lamella. The palatal plicae of *G. emigrans otanii* are more complex (usually Y-like) than those of the other two subspecies.

Measurements (in mm): D= 17.4–26.7, H= 7.0–8.3 (n=5).

Characters of the genital structure: Ethanol-preserved bodies are deposited in coll. PGB, respective shell in coll. JUO. Locality information: Guangxi, Yizhou Shi, Aishan Xiang, Xiannuyan, 172 m, 24°29.292'N, 108°34.057'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 13.11.2004. Three specimens were dissected. "Specimen1" had four parallel parietal plicae anterior to the single lamella, whereas both "Specimen2" and "Specimen3" had two vertical, "normal" lamellae. "Specimen1" and "Specimen2" had several embryos developing in their uterus. "Specimen3" was entirely aphyllid, having the proximal end of the vas deferens attached to the vagina near the genital opening. "Specimen3" had no embryos in its uterus, but had a spermatophore in its gametolytic sac, which is the indication of a successful mating.

The right ommatophoral retractor crosses the male and female genitalia. The penis of "Specimen1" was inflated, gradually tapering towards the end, "Specimen2" had a relatively slender penis with a thickening at its end; inner wall of "Specimen1" with parallel, longitudinal folds, of which some (2–4) are conspicuously thickened at the distal part of the penis; the penial wall of "Specimen2" was more complex, with the parallel folds forming "hollows" between each other. Penial caecum short, about one third of the length of the penis; retractor muscle attaches to the end of the penial caecum with several fibres, but some fibres attach at the base of the penial caecum on the distal end of the penis; the vas deferens-epiphallus transition is not conspicuous therefore the boundary between the two organs is not well visible; epiphallus about as long or a bit longer than the penial caecum. Vagina well-developed, its proximal part is inflated, its slimmer, distal part is slightly longer than the thicker proximal; vagina attached to the diaphragm with a several long, rather widely-spaced fibres; proximal part of vas deferens slender but distal end thickened; gametolytic sac and the additional organ next to the gametolytic sac are both very slender (gametolytic sac slightly thickened) and extremely long.

Radula: Figure 7.99 and Table 7.4.

Etymology: This subspecies is dedicated to Jamen Uiriamu Otani, the collector.

Type locality: Guangxi, Yizhou Shi, Shibie Xiang, Qingtan, 225 m, 24°23.719'N, 108°42.137'E.

Distribution: *G. emigrans otanii* is known from four locations in Northern Guangxi (Figure 7.110).

Remarks: The single shell from Baheng had four parallel plicae in front of the lamella on the parietal wall. The sample from Qingtan contained nine shells. Among them, two had four parallel plicae, more or less the same as in *G. emigrans quadrilamellatus*, and six other shells exhibited two lamellae, with horizontal plicae above and below the anterior lamella. In the ninth shell, anterior to the curved lamella, two oval plicae were connected to each other and located between the other horizontally short plicae. The plicae structure of Figure 8.26 (image on the middle) may be interpreted as the intermediate phenotype between those of Figure 8.26 (images on the left and right). Differences in shell lamellation within the same population are also very unusual in other land snail groups. Moreover, this aspect cannot be elucidated without knowledge of the genetic and ontogenetic background of lamella formation. The anatomical differences between the two different forms (ie. shell with four parallel, horizontal plicae and the shell with two lamellae) show only intraspecific variability (see under the Characters of the genital structure).

The shells collected at the cliffs above the Poliu Elementary School are unusually large (D=29–29.2 mm, n=2) and has only a single upper horizontal parietal plica anterior to the lamella (3 shells opened).

Gudeodiscus (Veludiscus) emigrans quadrilamellatus Páll-Gergely 2013

Figures 7.12, 7.47

- 1901b *Plectopylis emigrans* – Gude, Journal de Conchyliologie, 49: 206, Figs 5a–e, pl. 6 Figs 5a–c. (partim) ["Bac Kan", "Secteur de Nac-Ri", "Baie d'Along"]
- 1904 *Plectopylis quadrilamellata* "Möllendorff", — H. Fischer & Dautzenberg, Mission Pavie, Études diverses, III: 402. (nomen nudum)
- 1986 *Plectopylis quadrilamellata* "Möllendorff", — Richardson, Tryonia, 13: 20. (nomen nudum)
- 2008 *Plectopylis quadrilamellata* "Möllendorff", — Thanh, Sinh Hoc Journal of Biology, 30 (4): 6. (nomen nudum)
- 2013 *Gudeodiscus emigrans quadrilamellatus* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 15–17, Figs 27, 45a–b, 58 (map).
- 2015 *Gudeodiscus (Veludiscus) emigrans quadrilamellatus*, — Páll-Gergely et al., Zookeys 472: 65, Fig 6F, 13C–D.

Type material: Vietnam, Bắc Kạn Prov., Ba Bể Nat. Park, rd between Pac Ngoi and Bồ Lù, at Ba Bể Lake, left side off rd, 22°24.027'N, 105°37.426'E, leg. Hemmmmen, Ch. & J., 18.10.2009, holotype HNHN 97468, paratypes PGB/3; Vietnam, Tuyên Quang Prov., ca. 11 km from Son Doung to temple Tân Tráo, Cave Thia (right off old rd.), 21°46.194'N, 105°26.757'E, leg. Hemmmmen, Ch. & J., 25.10.2010, PGB/1; Vietnam, Bắc Kạn Prov., Ba Bể Nat. Park, Bồ Lù, harbour 600 m towards Pac Ngoi, right side of the road, 175 m, 22°23.989'N, 105°37.523'E, leg. Hunyadi, A., 19.11.2011. HA/10; Vietnam, Bắc Kạn Prov., Chợ Mới, eastern bank of the river, Khuôn Thung cross 500 m towards Xã Quảng Chu, right side of the road, 21°52.508'N, 105°47.328'E, leg. Hunyadi, 21.11.2011. HA/1; Vietnam, Chiem Hoa, Coll. Möllendorff, ex Fruhstorfer, SMF 150082/2; Vietnam, Tuyên Quang, Coll. Möllendorff, ex Fruhstorfer, SMF 150084/2; Central Tonkin, Chien-hoa, NHMUK 1901.12.23.39–40/2; Tonkin, Na-Ri, NHMUK 3/10/06(08?)/3; Tonkin, leg. Fruhstorfer, 30.10.1901, RBINS/1; secteur de Nac Ri leg. Messenger (n. 27), RBINS/2; Tonkin, Cho Ra, coll. Dukand, RBINS/2; Tonkin, Choa Ra, coll. Messenger, MNHN-IM-2012-2118/1+1 paratype with damaged aperture; Tonkin, leg. Fruhstorfer, 30.10.1901, RBINS/1; Pakhé (?), leg. Messenger, 1895–1915, MNHN-IM-2012-2119/1; (label not readable), leg. Messenger, 1895–1915, MNHN-IM-2012-2120/1; Vietnam, Na-Ri, leg. Messenger, 1895–1915, MNHN-IM-2012-2121/1; Vietnam, Tonkin, Bac Kan, leg. Messenger, MNHN-IM-2010-12118/1; Tonkin, MNHN-IM-2012-2122/1; Au Nord de Ha Noi, Tam Dao, MNHN-IM-2012-2123/3; Tonkin, coll Denis, MNHN-IM-2012-2124/2; Au Nord de Ha Noi, Tam Dao, MNHN-IM-2012-2125/15 adult paratypes and 6 juvenile paratypes; Nac-Ri, MNHN-IM-2012-2126/1; Ilots de la Baie d'Along, MNHN-IM-2012-2127/3, coll. Denis, 1946; Tonkin, slg. Bosch, C., ex Rolle, H., SMF 172098/3.

Museum material examined: Vietnam, Hạ Long Bay, leg. Messenger, MNHN-IM-2012-2320/1; Indochine, leg. Messenger, MNHN-IM-2012-2455/2; Tonkin, coll. Letellier 1949, MNHN-IM-2012-2448/1.

Diagnosis: A middle-sized, flat subspecies with conspicuous spiral sculpture and an elevated, sharp callus and sometimes an inconspicuous fold in the aperture. Parietal wall with a curved vertical lamella and four long horizontal plicae anteriorly.

Description: Shell chocolate brown or yellowish corneous; flat, only the apex is elevated from the surface of the shell; shell consists of 6–6.75 regularly growing whorls; suture moderately deep; teleoconch with very fine, irregularly wrinkled structure, but on the apical side and inside the umbilicus the spiral lines are more prominent; umbilicus very wide and moderately deep; body whorl rounded around the umbilicus; apertural lip whitish, thickened and slightly reflected; elevated callus slightly S-shaped, with two canals at both ends at the meeting points with the apertural lip; sometimes (in mature specimens) with an inconspicuous fold in the aperture, connected to the callus.

Seven specimens were opened belonging to different populations. Parietal wall with C-shaped, strong lamella; four long plicae anterior to the lamella; the last is the shortest, the second is the longest and the first and third are of the same length; plicae start close to the lamella, the second is in contact with it; palatal wall with six plicae, the first and the last are the shortest, the remaining four plicae are depressed Z-shaped or almost straight and oblique; there is an additional denticle above the posterior end of the last plica.

Differential diagnosis: *G. emigrans quadrilamellatus* differs from the nominotypical subspecies and *G. emigrans otanii* by the more prominent spiral sculpture. There can be a weak fold in the aperture of *G. emigrans quadrilamellatus*, which is in contact with the callus. The apertural fold of *G. emigrans otanii* however is stronger, always present and free from the callus. The nominotypical subspecies has only one horizontal denticle before the lamella, *G. emigrans otanii* usually has two lamellae and two horizontal plicae above and below the anterior one.

Measurement (in mm): D= 17.7–18.6, H= 7.1–7.6 (n=3).

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

Etymology: The name *quadrilamellatus* "Möllendorff" has never been published, however, used extensively in publications and in collections (probably all ex Möllendorff).

Type locality: Vietnam, Bắc Kạn Prov., Ba Bể Nat. Park, rd between Pac Ngoi and Bồ Lù, at Ba Bể Lake, left side off rd, 22°24.027'N, 105°37.426'E.

Distribution: *G. emigrans quadrilamellatus* is known from Bắc Kạn and Tuyên Quang provinces (Vietnam). I know this subspecies from two exact locations (see under types). Gude (1901b) mentions the species *emigrans* from the Halong Bay. In face of several samples received from different collectors, I have no reliable information on this species from the Halong area (Figure 7.110).

Remarks: *G. emigrans quadrilamellatus* was figured by Gude (1901b) under the name *Plectopylis emigrans* Möllendorff 1901. Gude examined the type specimen of *P. emigrans* but considered it a juvenile shell and thus, it had only a single plica anteriorly to the horizontal lamella. The other specimen in the Senckenberg Museum (SMF 9257, paratype from the same lot) however, has a well-developed aperture, but the upper three plicae are also

missing. It is important to mention, that juvenile shells of *G. emigrans quadrilamellatus* also have four anterior horizontal plicae and the anterior plicae are formed simultaneously (observed in the material of MNHN: "Vietnam N, Au Nord de Ha Noi, Tam Dao"). Consequently, I find it reasonable to describe the form bearing four horizontal parietal plicae under a new subspecific name.

***Gudeodiscus (Veludiscus) eroessi* Páll-Gergely & Hunyadi 2013**

2013 *Gudeodiscus eroessi* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 17.

2015 *Gudeodiscus (Veludiscus) eroessi*, — Páll-Gergely et al., Zookeys 472:59.

Diagnosis: A middle sized species with flat shell or somewhat elevated spire, glossy base, thin apertural lip, weak callus and missing apertural fold. Parietal wall with single lamella and two anteriorly located horizontal plicae with sometimes denticles in-between.

Differential diagnosis: Species belonging to the *G. phlyariius* group have roughly ribbed shell with sharp callus and two lamellae on the parietal wall. *G. eroessi* differs from *G. okuboi* in respect to shell smoothness and the lower, less prominent callus. *G. emigrans* has more prominently ribbed shell with usually an apertural fold, higher callus and more complex parietal lamellation. *G. eroessi* is smaller and possesses a much thinner shell than *G. pulvinaris*. The latter species usually has a fold in the aperture, which is lacking in *G. eroessi*. *G. multispira* is smaller, has more whorls and sometimes a small fold (denticle) in the aperture.

General distribution: The three subspecies of *G. eroessi* are known from northern Guangxi Province.

***Gudeodiscus (Veludiscus) eroessi eroessi* Páll-Gergely & Hunyadi 2013**

Figures 7.11, 7.48, 7.74, 7.90, 7.99

2013 *Gudeodiscus eroessi eroessi* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 17, Figs 21, 48a–d, 75 (map).

2014a *Gudeodiscus eroessi eroessi*, — Páll-Gergely & Asami, Genus 25(3): 533–536, Figs 8, 20F.

2015 *Gudeodiscus (Veludiscus) eroessi*, — Páll-Gergely et al., Zookeys 472:59, Fig. 34D–F, Tables 3, 6.

Type material: Guangxi, Guigang Shi, Guzhang Xiang, road to Xinan Cun, 23°21.549'N, 109°18.213'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.11.2004, holotype HNHM 97447, paratypes OK/5, PGB/1; Guangxi, Guigang Shi, Guzhang Xiang, road leading north from Chuanshan Cun, 160 m, 23°20.865'N, 109°19.169'E, leg. Hunyadi, A., 23.3.2011, NHMW 108166/1, SMF 341507/1, HA/15, PGB/6; Guangxi, Guigang Shi, Guzhang Xiang, hill slope behind Chuanshan Village, 177 m, 23°20.680'N, 109°19.098'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.11.2004, OK/6 PGB/2; Guangxi, Xingye Xian, Chenghuang Zhen, Longquanyan, 87 m, 22°36.600'N, 109°45.274'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 8.11.2004, OK/5, PGB/3; **20041109B** Guangxi, Guigang Shi, Guzhang Xiang, beyond Chuanshan Village, 153 m, 23°20.848'N, 109°19.256'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.11.2004, EZP/1, JG/1, OK/18, PGB/5; Guangxi, JH/4.

Diagnosis: A middle sized, flat, glossy subspecies with thin apertural lip and weak callus. On the parietal wall there is a single lamella with two anteriorly located horizontal plicae above and below and usually accompanied by two additional denticles in-between.

Description: Shell almost flat, with very slightly elevated spire; corneous, light brownish, thin, translucent; teleoconch with weak spiral structure; on ventral side spiral lines are missing, the shell is shiny. The 6–6.75 whorls are separated by relatively shallow suture; umbilicus wide and moderately deep; apertural lip relatively thin, slightly expanded; callus inconspicuous, present possibly only in old shells; there are canals at both ends of the callus; no fold in the aperture.

Eight specimens were opened from different populations. Parietal wall with one curved lamella with a horizontal plica above and a small denticle near the lower end anteriorly (the lower denticle often missing); between the two plicae there may be two additional denticles; palatal wall with six plicae; first thin and parallel with the upper suture; second plica longer and almost straight; last plica straight and slightly oblique, descending posteriorly; additional denticle near the posterior end of the last plica is present; remaining plicae depressed Z- or L-shaped.

Differential diagnosis: The upper and lower horizontal plicae before the parietal lamella are much longer in *G. okuboi*, which never has additional denticles between the horizontal plicae. These are however frequent in *G. eroessi eroessi*. For comparisons with *G. eroessi fuscus* and *G. eroessi hemisculptus*, see there.

Measurements (in mm): D= 15.0–19.2, H= 6.0–7.9 (n=5, shells from different localities).

Characters of the genital structure: Two specimens were anatomically examined. Both specimens had several embryos developing in the uterus. Ethanol-preserved body is deposited in coll. PGB, respective shell in coll. JUO. Locality information: **20041109B** Guangxi, Guigang Shi, Guzhang Xiang, beyond Chuanshan village, 153 m, 23°20.848'N, 109°19.256'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 09.11.2004.

The right ommatophoral retractor crosses the male and female genitalia. Penis rather long, its distal portion is inflated; inner wall of the proximal part smooth or with weak longitudinal folds all along the whole penis; inner wall of the distal penis part with several, slit-like pockets standing in a transversal row. The pockets did not contain calcareous crystals. Penial caecum well-developed, curved, internally with approximately 16 folds which may be wavy forming slit-like pockets for calcareous crystals, which were absent in the examined *G. eroessi eroessi* specimens, but were visible in *G. pulvinaris pulvinaris* specimens (see below). Epiphallus shorter than the penis, but its exact length is unknown due to the obscure boundary between the epiphallus and the vas deferens. Retractor muscle attaches at the lateral side of the tip of the penial caecum. Several additional muscle fibres attach to the distal end of the penis. Vagina slightly longer than the penis and epiphallus together; with weak vaginal bulb; several weak muscle fibres attach the vagina to the diaphragm. Gametolytic sac and the additional organ next to it are extremely long; gametolytic sac slightly thickened.

Radula: Figure 7.99 and Table 7.4.

Etymology: This species is dedicated to my friend, Zoltán Péter Eröss, (Budapest), malacologist.

Type locality: Guangxi, Guigang Shi, Guzhang Xiang, road to Xinan Cun, 23°21.549'N, 109°18.213'E.

Distribution: *Gudeodiscus eroessi eroessi* is known from central Guangxi. It frequently occurs together with *G. pulvinaris robustus* and *G. okubo* (Figure 7.112).

***Gudeodiscus (Veludiscus) eroessi fuscus* Páll-Gergely & Hunyadi 2013**

Figures 7.11, 7.48

2013 *Gudeodiscus eroessi fuscus* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 18, Figs 2 (map), 22, 49.

Type material: Guangxi, Hechi City, leg. Yang Hao, holotype HNHM 97448, paratypes HA/1, PGB/1; Guangxi, S-edge of Maolan Nature Reserve, at the border with Guizhou, S of Libo, leg. Whitten, T., September 2004, WM/1.

Diagnosis: A subspecies of *Gudeodiscus eroessi* with chocolate brown shell and a stronger, sharper callus with sometimes a small denticle (the specimen from the Maolan Nature Reserve had no denticle). There are one or two denticles in front of the vertical lamella on the parietal wall; the lower one (if present) is in contact with the lamella.

Differential diagnosis: *Gudeodiscus eroessi fuscus* is darker and flatter than the nominotypical subspecies. It has wider umbilicus, much stronger, slightly S-shaped callus and a small denticle in the aperture free from the callus.

Two specimens from the Hechi sample, and the only specimen from the Maolan Nature Reserve were opened. In the Hechi population, on the parietal wall there are two denticles anterior to the lamella, the lower one is attached (or situated very near) to the lamella. The single, corroded shell from the Maolan Nature Reserve had only one upper horizontal plica on the parietal wall. In *G. eroessi eroessi* there are usually four denticles and the lower one is far from the vertical lamella.

Measurements (in mm): D= 17.2–18.0, H= 6.7–6.9 (n=3).

Etymology: The Latin "fuscus" (= dark) refers to the colour of the shell, which is darker than that of the nominotypical species.

Type locality: Guangxi, Hechi City.

Distribution: *Gudeodiscus eroessi fuscus* is known only from two localities in northern Guangxi. No exact locality data were available; therefore the localities are indicated on Figure 7.108.

***Gudeodiscus (Veludiscus) eroessi hemisculptus* Páll-Gergely 2013**

Figure 7.11

2013 *Gudeodiscus eroessi hemisculptus* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 19, Figs 23, 75 (map).

Type material: Guangxi, Laibin Shi, Qidong Xiang, Ganchaoyan, 168 m, 24°00.791'N, 109°04.372'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 25.10.2011, holotype HNHM 97484; Guangxi, Laibin Shi, Qidong Xiang, north of Ganchaoyan, 24°01.249'N, 109°04.310'E, leg. Otani, J. U., 25.10.2011, paratypes JUO/2, PGB/1.

Diagnosis: A subspecies of *G. eroessi* with comparatively large aperture, somewhat elevated spire and strong dorsal sculpture which immediately turns into shiny, smooth surface at the middle of the body whorl.

Differential diagnosis: *G. eroessi hemisculptus* differs from the other two subspecies of *G. eroessi* by the relatively much larger aperture, the strong dorsal reticulated structure (dominated by spiral lines) and the smooth ventral surface. These structures change abruptly at the middle line of the body whorl.

One specimen was opened. It had one lamella on the parietal side and two horizontal plicae anteriorly; one above and one below.

Measurements (in mm, n = 3): D = 18.5, H = 7.9.

Etymology: *G. eroessi hemisculptus* is named after the two very different types of the shell sculpture (reticulated dorsally and smooth ventrally).

Type locality: Guangxi, Laibin Shi, Qidong Xiang, Ganchaoyan, 168 m, 24°00.791'N, 109°04.372'E.

Distribution: The subspecies is known only from two nearby localities in central Guangxi (Figure 7.112).

Remarks: Only one *Gudeodiscus* species is known with such an abrupt sculptural modification, namely, the Vietnamese *G. suprafilaris*, which has a more elevated spire, much narrower umbilicus and the palatal plicae are connected by a ridge.

Gudeodiscus (Veludiscus?) goliath Páll-Gergely & Hunyadi 2013

Figures 7.16, 7.44

2013 *Gudeodiscus goliath* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 22, Figs 2 (map), 35, 56a–b.

2015 *Gudeodiscus (Veludiscus?) goliath*, — Páll-Gergely et al., Zookeys 472:59.

Type material: Guangxi, Nanning City, ex coll. Yang Hao, holotype HNHM 97442, paratypes HA/1, PGB/1.

Diagnosis: A very large, flat species with a low fold in the aperture. Parietal wall with a single lamella with both anteriorly and posteriorly elongated ends.

Description: Shell yellowish, flat, strongly built; only the apex slightly elevated; 6.75–7 whorls are separated by shallow suture; teleoconch finely ribbed with a very fine spiral structure; umbilicus very wide; aperture relatively small with slightly thickened and expanded lip and low, S-shaped callus; canals at both ends at the junction with the lip; low apertural fold is free from the callus.

Two specimens were opened. Palatal wall with eight plicae; first and the last straight; first one parallel with the suture, but last one slightly oblique, descending posteriorly; above the distal end of the last plica there is an additional plicula; second plica dichotomously divided near its posterior end; remaining plicae simple and descending downwards.

Differential diagnosis: *G. goliath* is flatter than *G. pulvinaris robustus*, possesses a longer apertural fold and its lamella is supported anteriorly and posteriorly as well as above and below. It differs from both subspecies of *G. pulvinaris* by the vertical lamella having both ends elongated anteriorly and posteriorly.

Measurements (in mm): D= 27.4–28.1, H= 10.0–10.7 (n=3).

Etymology: This species is named after its remarkable size and impressive appearance.

Type locality: Guangxi, Nanning City.

Distribution: The species is known from the type locality only. No exact locality data were available; therefore the type locality is indicated on Figure 7.108.

Gudeodiscus (Veludiscus) okuboi Páll-Gergely & Hunyadi 2013

Figures 7.11, 7.48, 7.75, 7.90, 7.99

2013 *Gudeodiscus okuboi* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 24, Figs 20, 50a–b, 58 (map).

2014a *Gudeodiscus okuboi*, — Páll-Gergely & Asami, Genus 25(3): 538–540, Figs 11, 20C.

2015 *Gudeodiscus (Veludiscus) okuboi*, — Páll-Gergely et al., Zookeys 472:59.

Type material: Guangxi, Laibin Shi, Wushan Xiang, eastern end of Xiaopingyang Zhen, 130 m, 23°24.351'N, 109°10.029'E, leg. Hunyadi, A., 7.10.2009, holotype NHNM 97451, paratypes NHMUK 20120006/1, NHMW 108173/1, SMF 341511/1, HA/29, PGB/5; Guangxi, Guigang Shi, Laibin Xian, Wushan Xiang, near Wushan Liubei elementary school, 113 m, 23°23.69946'N, 109°14.13039'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 16.6.2005, OK/13, PGB/5; Guangxi, Xingye Xian, Chenghuang Zhen, Longquanyan, 87 m, 22°36.600'N, 109°45.274'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 8.11.2004, OK/3, PGB/1; **20041109A** Guangxi, Guigang Shi, Guzhang Xiang, road to Wushan Xiang, 131 m, 23°21.178'N, 109°17.432'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.11.2004, OK/7, PGB/2; Guangxi, Laibin Shi, Wushan Xiang, rock above Lubei Cun, 23°23.097'N, 109°14.074'E, leg. Hunyadi, A., 7.10.2009, HA/3, PGB/1; Guangxi, Laibin Shi, Wushan Xiang, Huangjin, 130 m, 23°24.20109'N, 109°13.20078'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 16.7.2006, EZP/1, JG/1, OK/23, PGB/3; Guangxi, Laibin Xian, Wushan Xiang, Huangjin, 122 m, 23°24.38925'N, 109°09.93131'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 16.7.2006, OK/8; Guangxi, Guigang Shi, Gu Zhang Xiang, rocky wall above Lianggu Cun, 140 m, 23°19.110'N, 109°14.405'E, leg. Hunyadi, A., 17.10.2009, HA/2.

Diagnosis: A small to medium-sized fragile, flat species with dense, sharp ribs; callus elevated without apertural fold. Parietal wall with a single lamella and two long horizontal plicae anteriorly above and below.

Description: Shell corneous, reddish-brownish or dark green; flat, with slightly elevated spire; teleoconch densely ribbed; the high, prominent ribs are equally visible on the apical and ventral surfaces; umbilicus wide and moderately deep; aperture with whitish, slightly reflected and thickened rim; callus slightly S-shaped; sharp, elevated, with canals at the two ends; there is no apertural fold.

Seven specimens were opened from different localities. Parietal wall with a single curved lamella and two long plicae above and below anteriorly; palatal wall with seven plicae; first and last short and straight; the remaining plicae with a break point near the posterior end; usually an additional plicula is present above the posterior end of the last plica.

Differential diagnosis: This species is easily recognisable due to the strong, dense ribs. It differs from *G. eroessi* by the more prominent sculpture (the difference is most conspicuous on the ventral side), sharper callus and longer plicae in front of the lamella. *G. okuboi* never has additional pliculae between the two horizontal plicae, but these denticles are often present in *G. eroessi*. *G. okuboi* is smaller and flatter than *G. pulvinaris robustus* and has a more pronounced surface sculpture.

The outer shell characters (sculpture, shell and umbilicus shape, palatal folds) of the Burmese Genus *dextrorsa* (Benson 1860) are very similar to those of *G. okuboi*. There are, on the other hand, large considerable differences in parietal lamellation; there is a long horizontal fold running up to the aperture in *dextrorsa*, which is never present in "Eastern Plectopylidae" species.

Measurements (in mm): D= 13.0–20.1, H= 5.5–7.4 (n=5, shells from different localities).

Characters of the genital structure: Two specimens were anatomically examined. "Specimen1" had several embryos developing in its uterus, "Specimen2" was not gravid. Ethanol-preserved bodies are deposited in coll. PGB, respective shell in coll. JUO. Locality information: **20041109A** Guangxi, Guigang Shi, Guzhang Xiang, road to Wushan Xiang, 131 m, 23°21.178'N, 109°17.432'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 09.11.2004.

The right ommatophoral retractor crosses the male and female genitalia. Penis rather long, gradually tapers to the end; internally with weak longitudinal folds all along the whole penis and pockets on the wall of the thickened, distal part; the pockets did not contain calcareous crystals; one portion of the penis wall was more conspicuously thickened than the other parts of the penis; penial caecum relatively short and thick, internally with two well-visible folds; epiphallus shorter than the penis, but its length is unknown due to the obscure boundary between the epiphallus and the vas deferens; retractor muscle attaches at the end of the penial caecum, and several additional muscle fibres attach to the distal end of the penis. A muscle fibre is visible between the middle section of the penial caecum and the distal end of the penis. Vagina slightly longer than the penis and epiphallus together, with well-developed vaginal bulb; several weak muscle fibres attach the vagina to the diaphragm. Gametolytic sac and the additional organ next to it are extremely long; gametolytic sac thickened.

Radula: Figure 7.99 and Table 7.4.

Etymology: This species is named after Kanji Okubo, the collector.

Type locality: Guangxi, Laibin Shi, Wushan Xiang, eastern end of Xiaopingyang Zhen, 130 m, 23°24.351'N, 109°10.029'E.

Distribution: The species is known from Southern Guangxi. It lives frequently together with *G. pulvinaris robustus* and *G. eroessi* (Figure 7.110).

Gudeodiscus (Veludiscus) pulvinaris (Gould 1859)

2015 *Gudeodiscus (Veludiscus) pulvinaris*, — Páll-Gergely et al., Zookeys 472:59.

Diagnosis: A medium-sized to very large species with flat or somewhat elevated spire, strongly built shell and a small denticle in the aperture. Palatal plicae depressed "Z"-shaped; parietal wall with a lamella and usually two short horizontal plicae anteriorly (sometimes missing).

Differential diagnosis: *G. eroessi* has a more fragile, thinner shell and usually additional denticles between the horizontal plicae on the parietal wall. *G. okuboi* has prominent, dense ribs.

General distribution: *G. pulvinaris* is reported from Guangxi and southern Guangdong.

Gudeodiscus (Veludiscus) pulvinaris pulvinaris (Gould 1859)

Figures 7.16, 7.76, 7.95, 7.100

- 1859 *Corilla pulvinaris* Gould, Proceedings of the Boston Society of Natural History, 6: 424 ["Hong Kong, high up in the ravines; also near Kanton."].
- 1867 *Helix pulvinaris*, — Martens, Die Preussische Expedition Nach Ost-Asien.: 51, pl. 14, Fig. 9 ["Hongkong" and "Kanton"].
- 1868 *Helix pulvinaris*, — L. Pfeiffer, Monographia heliceorum viventium., 5: 399.
- 1883 *Plectopylis pulvinaris*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 10: 376, pl. 12, Fig. 9 ["in Insula Hongkong ad rupes altiores (1500') and "ad urben Canton" and "in insula Lantou"].
- 1885a *Plectopylis pulvinaris*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 12: 388.
- 1885a *Plectopylis pulvinaris* var. *continentalis* Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 12: 388–389 ["Ma-an-shan nordnord-östlich von Hongkong an der Mirs-Bay"] nov. syn.
- 1886 *Plectopylis pulvinaris*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 189.
- 1887 *Helix pulvinaris*, — Tryon, Manual of Conchology, 2 (3): 157, pl. 33, Figs 29–31 [Hong Kong and Canton, China].
- 1896d *Plectopylis pulvinaris*, — Gude, Science Gossip, 3: 180, Fig. 25.
- 1896d *Plectopylis pulvinaris* var. *continentalis*, — Gude, Science Gossip, 3: 180.
- 1899e *Plectopylis (Sinicola) pulvinaris*, — Gude, Science Gossip, 6: 148.
- 1899e *Plectopylis (Sinicola) fimbriosa* v. *continentalis* (!), — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Sinicola) pulvinaris*, — Gude, Science Gossip, 6: 176.
- 1939 *Plectopylis pulvinaris*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112, pl. 11, Fig. 12.
- 1939 *Plectopylis pulvinaris continentalis*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112, pl. 11, Fig. 13.
- 1944 *Plectopylis pulvinaris*, — Yen, Proceedings of the California Academy of Sciences, 4th series, 23 (38): 581, Plate 51, Fig. 39.
- 1964 *Plectopylis (Plectopylis) pulvinaris*, — Johnson, The recent Mollusca of Augustus Addison Gould: 134, Plate 36, Fig. 8.
- 1996 *Plectopylis pulvinaris pulvinaris*, — Hoo, Tentacle, 6: 13 [Hongkong, Plantation Road and Mt. Austin].
- 2013 *Gudeodiscus pulvinaris pulvinaris*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 29, Figs 2 (map), 38–39.
- 2014a *Gudeodiscus pulvinaris pulvinaris*, — Páll-Gergely & Asami, Genus 25(3): 541, Figs 12, 21H.

Types examined: China: Ma-an-shan, Kwangtung, Slg. Möllendorff, lectotype of *Plectopylis pulvinaris* var. *continentalis* Möllendorff, SMF 9270; China: Ma-an-shan, Kwangtung, Slg. Möllendorff, paralectotypes of *Plectopylis pulvinaris* var. *continentalis* Möllendorff, SMF 9271/3; Hong Kong, coll. Gould, MCZ 169316 (lectotype of *pulvinaris*).

Museum material examined: China: Hongkong, Slg. Kobelt ex Möllendorff, SMF 42720/6; China: Hongkong, Slg. Möllendorff, SMF 42718/6+1; China: Hongkong, Slg. W. Kobelt (alte Schau-Slg.) ex Möllendorff 1882 + Gerlach, SMF 42722/3; China: Hongkong, (Lan-dau), Slg. Möllendorff, SMF 42721/1; China: Hongkong, Slg. C. Boettger, 1903, SMF 102822/6; China: Macao (Macau), Slg. O. Boettger ex G. Ehrenbach, 1887, SMF 42719/2; China: Hongkong, Slg. C. Boschex H. Rolle (W. Schluter), SMF 172106/2; China: Hongkong, Slg. Jetschin ex B.

Schmacker, 1928, SMF 102821/1; China: Hongkong, Slg. Möllendorff, SMF 42718/5; Slg. H. Kaltenbach, SMF 294870/1; China: Hoi-Kow, Lung-shun-wan, Kwangtung, Krejci-Graf S. 1933, SMF 42723/1; NHMW no number Pf VII. 3213/1; Hongkong, Coll. Gerstenbrandt, NHMW 4509/1; Hong Kong, Coll. Rušnov ex coll. dr. W. Blume, NHMW/4; Hong-Kong Peak 86.4.19.42–50, NHMUK 1886.4.19.42–50/9; Hong Kong, Salisbury ex. Bedomme, NHMUK 20110362/3; Hong Kong, Int. Austen, NHMUK 1937.12.30./3842–47/6; Hong Kong, NHMUK 1916.3.16.12/1; Victoria Peak, Lugard Rd., Hong Kong, 12.1982. A. J. Brandt Colln., NHMUKw; Hong Kong Island, Victoria Peak, North Face, Lugard Rd., in wooded area, under litter next to pipeline, 11.7.1982, A. J. Brandt Colln., NHMUKw; A. J. Brandt Colln., NO 38A, C/F, NHMUKw; Hong Kong, Coll. Staadt, 1969, MNHN/1; Hong Kong, Coll. Denis, MNHN/1+2; Hong Kong, Coll. Letellier, 1949, MNHN/1; Hong Kong, Coll. Jousseume, MNHN/2; Hong Kong, Coll. Fischer, MNHN/2; China, ZMB/MOLL 98922/1; Hongkong, Schmacker, RBINS/1; Hongkong, Kobelt, 6.3.86, RBINS/5; Hong Kong, coll. Dr. Brancsik, ex coll. Mus. Berlin, NHMSB 131/203, 122816–122817 (2 specimens); China, Hong Kong, coll. Eastlake, J. W., USNM 161709/6; China, hilltop near Hong Kong, ex coll. Hungerford, USNM 47923, one juvenile and 2 adult shells; China, Hong Kong, ex coll. Hungerford, USNM 161710/7; China, Hongkong, Chamberlain coll., ex coll. Quadras, USNM 609148/1; China, Hong Kong, ex coll. Kobelt, USNM 124553/1; China, Hong Kong, coll Henderson, ex coll. Schmacker, USNM 319264/4; Hongkong coll. Borcherdindex Möllendorff, SMNG 07806/6; Hongkong coll. Borcherdindex Möllendorff, SMNG 8060/3; Hongkong 1500', ex coll. Möllendorff (gift), SMNG 12607/1; Hong Kong, leg. Schmacker, Altonaer Museum, ZMH 45902/2.

New material examined: Hong Kong, Victoria, near the Upper Peak Tram Station, leg. Podani, J., 1991 October, PJ/2; Hong Kong Peak, leg. Miu Yeung, June 2013, PGB/6 (anatomically examined).

Diagnosis: A medium-sized, flat species with a small denticle in the aperture. Palatal plicae have depressed "Z"-shape; parietal wall with one lamella and one denticle in front of the lamella.

Description: Shell flat, brown-yellowish, slightly glossy; dorsal part of teleoconch irregularly wrinkled; less conspicuous spiral sculpture also present; whorls 5.5–6; separated by rather deep suture; umbilicus very wide; aperture relatively large; peristome white and expanded with one small denticle; callus present in only a few specimens (probably old individuals).

Two opened specimens were observed. Parietal wall with one strong lamella usually accompanied by a short plica below and above anteriorly; palatal wall with seven plicae; first and the last parallel with the suture; others have depressed Z-shape; additional plicae may present, often between the last and the penultimate plicae.

Differential diagnosis: *G. pulvinaris pulvinaris* is smaller, flatter and has a weaker apertural fold and callus than *G. pulvinaris robustus*.

Measurements (in mm): D= 17.0–18.2, H= 5.7–6.3 (n=3, SMF 4270).

Characters of the genital structure: Two specimens collected at the Hong Kong Peak by Miu Yeung in June 2013, were anatomically examined. Specimens are deposited in the PGB collection. The genital anatomy of *G. pulvinaris pulvinaris* does not differ notably from that of *G. pulvinaris robustus* Páll-Gergely & Hunyadi 2013. This confirms their close relationship and supports their subspecific status to each other.

The dissected *G. pulvinaris robustus* specimen (see Páll-Gergely & Hunyadi 2013) had developing embryos in its uterus, and had no calcareous crystals or granules within the penis lumen, whereas the *G. pulvinaris pulvinaris* specimens examined this time were not gravid and had several translucent claws within the "pockets" on the wall of the distal part of the penis. Additionally, the *G. pulvinaris pulvinaris* specimens had similar, but smaller calcareous claws between the folds inside the penial caecum.

Radula: Figure 7.100 and Table 7.4.

Distribution: *P. pulvinaris pulvinaris* is known from Hainan, Hongkong, Guangdong and Maanshan (loc. typ. of *pulvinaris continentalis*) (Figure 7.108).

Remarks: "*P. pulvinaris continentalis*" is larger and darker than the nominotypical subspecies according to Möllendorff (1885a). This may be true for the lectotype, but the paralectotypes are smaller and lighter. *P. pulvinaris continentalis* falls into the variation of *P. pulvinaris pulvinaris* and is therefore, considered a synonym of *P. pulvinaris pulvinaris*.

Gudeodiscus (Veludiscus) pulvinaris robustus Páll-Gergely & Hunyadi 2013

Figures 7.16, 7.44, 7.77, 7.95

2013 *Gudeodiscus pulvinaris robustus* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 30, Figs 36–37, 47a–b, 59 (map), 60a–b.

Type material: Guangxi, Guigang Shi, Guzhang Xiang, 600 m from Shajiang-Lianggu Cun cross, Lianggu Cun, 160 m, 23°19.062'N, 109°15.122'E, leg. Hunyadi, A., 17.10.2009, holotype HNHM 97439, paratypes NHMW 108169/1, SMF 341514/1, NHMUK 20120002/1, HA/39, PGB/6; Guangxi, Yulin Shi, Xingye Xian, Chenghuang Zhen SE 2 km, Lufengshan Scenic Area, 22°36.814'N, 109°45.457'E, leg. Hunyadi, A., 5.10.2009, HA/19, PGB/4; Guangxi, Guigang Shi, Gu Zhang Xiang, eastern edge of Sha Cun–Litang Cun, 140 m, 23°18.816'N, 109°16.211'E, leg. Hunyadi, A., 17.10.2009, HA/6, PGB/2; Guangxi, Guigang Shi, Gu Zhang Xiang, rocky wall above Lianggu Cun, 140 m, 23°19.110'N, 109°14.405'E, leg. Hunyadi, A., 17.10.2009, HA/6, PGB/2; Guangxi, Laibin Shi, Wushan Xiang, rock above Lubei Cun, 23°23.097'N, 109°14.074'E, leg. Hunyadi, A., 7.10.2009, HA/4; Guangxi, Guigang Shi, Guzhang Xiang, environment of Pan Cun cross, 130 m, 23°19.072'N, 109°17.320'E, leg. Hunyadi, A., 17.10.2009, HA/4; Guangxi, Guigang Shi, Laibin Xian, Wushan Xiang, near Wushan Liubei elementary school, 113 m, 23°23.69946'N, 109°14.13039'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 16.6.2005, OK/49, PGB/10; Guangxi, Guigang Shi, Guzhang Xiang, SE of the crossroad beyond Cui Cun, 142 m, 23°16.62527'N, 109°15.69951'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 16.6.2005, OK/8, PGB/1; Guangxi, Xingye Xian, Chenghuang Zhen, Longquanyan, 87 m, 22°36.600'N, 109°45.274'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 8.11.2004, PGB/2+2; Guangxi, Neibi, Guigang Shi, Guzhang Xiang, 128 m, 23°16.51346'N, 109°14.53144'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 16.6.2005, OK/6, PGB/5; Guangxi, Laibin Shi, Wushan Xiang, Xinan She, leg. Ohara, K., Okubo, K. & Otani, J. U., 21.12.2003, PGB/2; Guangxi, collected by local collectors, 2008, ex coll. He Jing, PGB/2; Guangxi, collected by local collectors, ex coll. He Jing, PGB/3; Guangxi, Guilin city, leg. YangHao, PGB/2; Guangxi, Wuxuan Xian, Tongwan Zhen, Hengshan, 65 m, 23°22.848'N, 109°33.836'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 10.11.2004, OK/2; Guangxi, Guigang Shi, Guzhang Xiang, road to Xinan Cun, 23°21.549'N, 109°18.213'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.11.2004, OK/1; Guangxi, near Liuzhou, ex coll. Marcus Coltro, JG/2; Guangxi, JH/12; Guangxi, ex coll. Hemmen, J., PGB/5, Guangxi, ex coll. Zhao Yifan, EZP/4; Guangxi, Nandan Xian, Lihuyaozu Xiang, En Cun, 614 m, 25°03.355'N, 107°36.280'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 20.10.2011, OK/1; Guangxi, Huanjiangmaonan zu Zizhixian, Sien Zhen, Neinan, 299 m, 24°49.562'N, 108°09.193'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 19.10.2011, OK/1, PGB/1; Guangxi, Duanyaozu Zizhixian, Baoan Xiang, Nongjiao, 607 m, 24°05.580'N, 107°46.971'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 24.10.2011, OK/2, PGB/1; Guangxi, JG/1.

Diagnosis: A large or very large, variable *Gudeodiscus* subspecies with a slightly elevated spire, thick callus and denticle in the aperture. On the parietal wall there is a lamella and usually two short horizontal plicae anteriorly (sometimes missing).

Description: Shell depressed conical (some shells are totally flat); yellowish or brownish corneous; consists of 7.25–7.75 regularly growing whorls, which are separated by a moderately deep suture; teleoconch has irregular wrinkled sculpture with spiral lines; sometimes in fresh shells, fine periostracal folds can be seen near the suture; ventral side of the shell is much smoother; umbilicus very wide and deep; the last whorl rounded dorsally around the umbilicus; aperture relatively large; with white, conspicuously thickened and reflected lip; callus typically lower and thinner than the lip; usually a short fold is present in the aperture and is free from the callus; possibly more mature specimens possess a thicker apertural lip and a stronger callus and fold.

More than ten specimens were opened from different locations. On the parietal wall there is a curved vertical lamella and usually two denticles (short plicae) anteriorly; one above and one below. In some populations (e.g. Xinanshe), the denticles are missing while only the lamella is present. On the palatal wall there are six or seven plicae; usually additional pliculae can be seen above the dorsal end of certain plicae (most frequently above the last plica); first and last plicae are always slender; straight and parallel with the sutures; remaining plicae have depressed Z- or L-shape.

Differential diagnosis: *Gudeodiscus pulvinaris robustus* is larger and has a more elevated spire than the nominotypical subspecies. Additionally, it has a well-developed callus, which is very rare in *G. pulvinaris pulvinaris* (only old specimens have a somewhat thickened callus).

Measurements (in mm): D= 20.5–31.2, H= 7.8–10.7 (n=8, shells from different localities).

Characters of the genital structure: One specimen was dissected (Guangxi, Guigang Shi, Guzhang Xiang, eastern edge of Sha Cun – Litang Cun, 140 m). The dissected specimen had several eggs inside the uterus. The eggs contained well-developed offspring (up to 4 whorls). The right ommatophoral retractor crosses the genitalia. Penis cylindrical with a slimmer proximal and a thicker distal portion; the two portions are about of the same size; inner penis wall ribbed; ribs are visible on the distal part of the penis; no hooks found in the penis lumen. Penis slightly shorter than the epiphallus, and almost three times longer than the penial caecum; retractor muscle thick, attaches to the penial caecum. Proximal part of the penis, the insertion of the retractor muscle on the penial caecum and the

proximal portion of the epiphallus are covered by a moderately strong sheath. Vas deferens very long; vagina with several muscle fibres on one side, but its base is without swelling. The gametolytic sac very slender.

Etymology: The name "robustus" refers to the strongly built shells.

Type locality: Guangxi, Guigang Shi, Guzhang Xiang, 600 m from Shajiang-Lianggu Cun cross, Lianggu Cun, 160 m, 23°19.062'N, 109°15.122'E.

Distribution: *Gudeodiscus pulvinaris robustus* is relatively common within its distribution area in Guangxi (Figure 7.111).

Genus *Halongella* Páll-Gergely Páll-Gergely 2015

2015 *Halongella* Páll-Gergely et al., Zookeys 473: 65.

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

Content: *fruhstorferi* (Möllendorff 1901) and *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 anterior 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)* 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*. 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. Genus3 lacks an epiphallus and has dense, wavy ribs on the protoconch. In contrast, *Halongella* has a well differentiated epiphallus and has relatively widely-spaced, straight ribs on the embryonic whorls.

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

Distribution: The two species of the genus *Halongella* inhabit the Halong Bay area (northern Vietnam) only (Figure 7.129).

Halongella fruhstorferi (Möllendorff 1901)

Figures 7.5, 7.45, 7.78, 7.90, 7.95, 7.102

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

1901a *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.

2015 *Halongella fruhstorferi*, — Páll-Gergely et al., Zookeys 472:67, Figs 7D, 9O, 14O–R, 25, 29C, 29I, 32A–B, 36A–C

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

Museum material examined: Tonkin, Kebao (Insel), SMF150081/2; 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°03.530'N, 107°25.390'E, leg. Hemmen, Ch. & J., 14.08.2011., HE/23, HA/1, PGB/3.

Diagnosis: Shell small, solid, thin-walled, almost flat and smooth, with weak apertural lip and sometimes a small apertural denticle. Parietal wall with one parietal lamella with two short horizontal plicae anteriorly, one above and one below; palatal plicae short, oblique, depressed Z-shaped.

Differential diagnosis: *Halongella fruhstorferi* and *H. schlumbergeri* are congeneric based on similarity of genital morphology. *H. fruhstorferi* is smaller than *H. schlumbergeri*, having a more fragile, lighter shell and weaker apertural lip and apertural fold. In shape, *H. fruhstorferi* resembles to *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. *G. phlyarius* and the similar species (*G. anceyi*, *G. hemmeni* u. sp., *G. messengeri*) have a well-developed anterior lamella or denticles at the position of the anterior lamella.

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

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

Characters of the genital structure: One specimen was examined anatomically. Locality: Vn11-171 Quảng Ninh Province, Vân Đồn Island (NE Cẩm Hà), Cái Rồng village, 21°3.560'N, 107°25.551'E, leg. Hemmen, Ch. & J., 14.08.2011.

Penis relatively long, spindle-shaped, inner wall with several (at least 20) parallel running folds; 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; 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; 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.

Radula: Figure 7.102 and Table 7.4.

Distribution: The species is known only from Kebao Island (Hà Long Bay area) (Figure 7.115).

Halongella schlumbergeri (Morlet 1886a)

Figures 7.5, 7.45, 7.79, 7.90, 7.94–7.95, 7.102, 7.133

- 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 la Société Malacologique de France, 4: 101–102.
- 1887b *Plectopylis jovia* Mabille, Bulletin de la 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, Pl. 43, Figs 36–39.
- 1894 *Plectopylis jovia*, — Pilsbry, Manual of Conchology...: 146., Plate 40, Figs 1–4.
- 1897j *Plectopylis schlumbergeri*, — Gude, Science Gossip, 4: 138., Figs 58a–b. ["Halong Bay and Elephant Mountain, Tonkin"].
- 1897j *Plectopylis jovia*, — Gude, Science Gossip, 4: 138–139., Figs 59a–b. ["Halong"].
- 1899b *Plectopylis schlumbergeri*, — Gude, Science Gossip, 5: 332.
- 1899b *Plectopylis jovia*, — Gude, Science Gossip, 5: 332.
- 1899e *Plectopylis (Endoplon) schlumbergeri*, — Gude, Science Gossip, 4: 148.
- 1899e *Plectopylis (Endoplon) jovia*, — Gude, Science Gossip, 4: 148.
- 1899f *Plectopylis (Endoplon) schlumbergeri*, — Gude, Science Gossip, 6: 175.
- 1899f *Plectopylis (Endoplon) jovia*, — Gude, Science Gossip, 6: 175.
- 1901b *Plectopylis (Endoplon) hirsuta* Möllendorff **new synonym**, Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 33 (5/6): 114–115. ["in insula Bah-mun"]
- 1901b *Plectopylis Schlumbergeri*, — Gude, Journal de Conchyliologie, 49: 199.
- 1901b *Plectopylis Villedaryi*, — Gude, Journal de Conchyliologie, 49: 212. ["Llots de la baie d'Along"]
- 1901c *Plectopylis jovia*, — Gude, Journal of Malacology, 8: 47–48., Figs 1a–b.
- 1901c *Plectopylis schlumbergeri*, — Gude, Journal of Malacology, 8: 47–48., Figs 2a–b.
- 1901c *Plectopylis villedaryi*, — Gude, Journal of Malacology, 8: 47–48., Figs 3a–b.

- 1901a *Plectopylis pilsbryana* Gude, Journal of Malacology, 8: 110., **new synonym** ["Lang-Son, Bac-Ninh (Vathelet). Isles in Along Bay (Messenger). Tonkin (Fruhstorfer)"]
- 1901a *Plectopylis (Endoplion) hirsuta*, — Gude, Journal of Malacology, 8: 111–112., Figs 1a–f. ["Island Bah-Mung"]
- 1901a *Plectopylis (Endoplion) 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.
- 2015 *Halongella schlumbergeri*, — Páll-Gergely et al., Zookeys 472:71, Figs 6A–D, 9M–N, 14H–N, 26, 29A–B, 29H, 30G–I, 33A–G, 36D–F, 45B.

Types examined: Llots de la Baie d'Along, leg. Messenger (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*); Tonkin, NHMUK 1922.8.29.52 (holotype of *pilsbryana*); Tonkin, MNHN 24582 (2 syntypes of *schlumbergeri*); Tonkin, Bah-Mun, coll. Möllendorff ex Fruhstorfer, SMF 9277 (lectotype of *hirsuta*); same data, SMF 9278 (2 paralectotypes of *hirsuta*).

Museum material examined: Tonkin, That-Khé, coll. Dosch ex Rolle ex Messenger, 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 Fruhstorfer 130, SMF 150129/2; Tonkin, Hai-fong, coll. Möllendorff ex Fruhstorfer, 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'Along, excoll labo. de Géologie de la Sorbonne (entrée 1952), MNHN-IM-2012-2271/2; Baie d'Along, 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-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. Messenger, MNHN-IM-2012-2316/1; Halong Bay, leg. Messenger, MNHN-IM-2012-2317/4; Halong Bay, leg. Messenger, 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, MNHN-IM-2012-2368/2; Halong Bay, leg. Messenger, MNHN-IM-2012-2369/3; Halong Bay, leg. Messenger, MNHN-IM-2012-2370/3; Halong Bay, leg. Messenger, MNHN-IM-2012-2375/6; Tonkin, coll. Fischer, ex Crosse, MNHN-IM-2012-2380/2; Ilots de la Baie d'Along, leg. Messenger, MNHN-IM-2012-2381/2; Tonkin, leg. Messenger, 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, 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 Messenger, 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 Bàu, 162 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 Bàu, 97 m, 20°47.81769'N, 107°00.42256'N, leg. Ohara, K., 22.11.2007., OK/4, PGB/1; **20081118A** Quảng Ninh Province, Hạ Long Bay, Đầu Gỗ Isl., near Đầu Gỗ Cave, 13 m, 20°54.696'N, 107°01.069'E, leg. Ohara, K., 18.11.2008., OK/14, PGB/2; **GS25** Quảng Ninh Province, 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 Bàu 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 Đò 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 Đò Isl., NE coast, 20°52.44'N, 107°12.10'E, leg. Vermeulen, J., 03.10.2003., coll. Maassen, W. J. M. (2 shells); **MAA3** Quảng Ninh Province, Hạ Long Bay Area, unnamed island in Cống Đò 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 Éch, 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 Éch 500 m towards Mây Bàu, 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, Đảo Trà 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, Đảo Trà Bản (island), Cảng Bản Sen (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. 28 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; **VERMI** 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, Primary 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.

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 plicae) and well-developed posterior lamella; palatal plicae depressed Z-shaped.

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

Measurements (in mm): D= 16.6–17.1, H= 8.3–8.5 (n=2, Maassen 5); D= 17.4–19.9, H= 7.9–9.2 (n=2, Maassen4); D= 16.1–19.8, H= 7–9.4 (n=2, Maassen 6); D= 23.1–23.4, H= 10.8–11 (n=2, 2008.11.19A); D= 24.8–25.6, H= 11.7–13 (n=4, Vn11-174); 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 Map6.

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

Characters of the genital structure: 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); "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).

Penis relatively long, slimmer proximally and slightly thicker distally; inner wall with several (16–18) parallel running folds; between the folds flat, T-shaped calcareous granules were found (both specimens had granules between the folds); 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; 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; "Specimen1" had tiny rounded granules ("sand") in the vagina lumen, not attached to the vagina wall (Figure 33F); stalk of the gametolytic sac with conspicuously thickened gametolytic sac is longer than the much slimmer diverticulum.

Radula: Figure 7.102 and Table 7.4.

Distribution: The species has only been recorded in the Hạ Long Bay area (Hải Phòng and Quảng Ninh provinces) (Figure 7.115 and Figure 7.118).

Remarks: Gude (1901c) 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. I had the possibility to observe and measure a number of shells collected in the Hạ Long Bay Area and provided with exact GPS data. I found that the shells characters exhibit little variation other than in size. Therefore, I 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). I therefore synonymize *Plectopylis hirsuta* with *Halongella schlumbergeri*.

Genus3, u. gen.

Type species: *Helix laomontana* L. Pfeiffer 1862.

Content: *laomontana* (L. Pfeiffer 1862).

Diagnosis: Shell flat, widely umbilicated, body whorl rounded; protoconch with dense, regular, slightly waved ribs. Epiphallus absent, diverticulum shorter than the gametolytic sac.

Differential diagnosis: All other genera of Tribe2 has a well distinguished epiphallus. See also under Genus2, *Gudeodiscus* and *Halongella*.

Etymology: The new genus is dedicated to Fred Naggs (NHMUK) in acknowledgement of his help with my studies on the Plectopylidae.

Distribution: Northern Laos, maybe Cambodia (Figure 7.129).

Genus3 *laomontana* (L. Pfeiffer 1862)

Figures 7.4, 7.30, 7.80, 7.92, 7.98

1862 *Helix laomontana* L. Pfeiffer, Proceedings of the Zoological Society of London, 272, pl. 36, Figs 9–10 [Lao Mountains, Camboja].

1863 *Helix laomontana*, — L. Pfeiffer, Novitates Conchologicae 2: 216, pl. 57, Figs 7–9.

1868 *Helix laomontana*, — L. Pfeiffer, Monographia Heliceorum Viventium...: 394.

1875b *Helix (Plectopylis) laomontana*, — Godwin-Austen, Proceedings of the Zoological Society of London: 612.

1887 *Helix laomontana*, — Tryon, Manual of Conchology, 2 (3): 160, pl. 34, Figs 60–62.

1897b *Plectopylis laomontana*, — Gude, Science Gossip, 3: 245, Figs 36a–c.

1899e *Plectopylis (Chersaecia) laomontana*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Chersaecia) laomontana*, — Gude, Science Gossip, 6: 175.

1914b *Plectopylis (Chersaecia) laomontana*, — Gude, The Fauna of British India including Ceylon and Burma. Mollusca.—II. (Trochomorphidae-Janellidae): 73.

1920 *Plectopylis laomontana*, — Gude, Journal of Molluscan Studies, 14: 62, Fig. 1.

2013 *Chersaecia laomontana*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 7–8.

Types examined: Cambodia, NHMUK 20130004 (3 syntypes).

Museum material examined: Laos, Luang Prabang (alte Schau-slg.), SMF 150121/2; Laos (Siam), Luang Prabang, ex Möllendorff, SMF 294866/3; Laos, Luang Prabang slg. Dosch ex H. Rolle, SMF 172067/1; Laos, Luang Prabang, SMF 150122/4; Cambodia, slg. Dosch ex H. Rolle ex Sowerby ex Fulton, SMF 172068/3; Laos, Luang Prabang, Französ. Hinterindien, C. Boettger 1904/43, SMF 102819/3; Cambodia, NHMW 342232/2; Laos, Lao Mountains, Altonaer Museum, coll. Semper, O. ex Cuming, ZMH 45901/2; Cambodge, coll. Achat Lallé, 1870, MNHN 2012-2506/1; Louang Prabang, MNHN 2012-2507/1; Cambodge, coll. Deshayes in coll. Crosse, MNHN 2012-2508/1; Laos, coll. Denis, MNHN 2012-2509/1; Louang Prabang, coll. Morgan, MNHN 2012-2510/2; Mts. Lao, Cambodja, MNHN 2012-2511/1; Louang Prabang, coll. Letellier 1949, MNHN 2012-2512/1; Louang Prabang (Laos), coll. Morlet-Fischer, MNHN 2012-2513/4; Louang Prabang (Laos), coll. Staadt 1969, MNHN 2012-2514/2; Louang Prabang (Laos), coll. Morlet-Fischer, MNHN 2012-2515/2; China, coll. Salisbury ex Beddome (also Canon Hoisley coll., 1918), NHMUK 20110363; Cambojia, Mr. Mouhot, Lao Mountains, NHMUK/3; Siam, Lao Mountains, coll. Godwin-Austen, NHMUK/2; India, NHMUK/2; Camboja, NHMUK/1.

New material examined: 2006.10.13. Laos, Luang Prabang Province, Ban Pak Ou, Nam Wu (opposite side of Ban Pak Ou), 364 m 20°03.48276'N, 102°12.79912'E, leg. Ohara, K. 13.10.2006., PGB/5; Laos, Tad Kuangsi Waterfall, about 20 km SW of Luang Prabang, 19°43'02.97"N 101°59'38.68"E., leg. Reischütz, A., February 2010. (3 spec.); Laos, Tad Kuangsi Waterfall, about 20 km SW of Luang Prabang, 19°43'02.97"N 101°59'38.68"E, leg. Theisl, T. April 2009. (3+2 juv.); Laos, Luang Prabang Province, Tad Kuangsi Xi (Waterfall), 466 m, 19°44.96071'N, 101°59.49286'E, leg. Ohara, K. 14.10.2006., PGB/1; **16L06**, S of Luang Prabang ~7 km, Near Tad Thong waterfall, Luang Prabang province, central Laos, Limestone, clay, under rocks and logs in old forest near stream, 19°50.064'N; 102°07.755'E; alt. 431 m, 10x200 m, 14:30–15:30, 3 November 2006, Ahmed Abdou, Igor V. Muratov.

Diagnosis: A dextral, medium-sized or large species with a rounded body whorl, and no apertural fold. On the parietal wall there is a single curved lamella.

Description: The yellowish, sometimes pink or light brown shell is dextral, almost flat with the apex slightly elevated. The 5.5–6 whorls are separated by a moderately deep suture. The protoconch is very densely, regularly ribbed, there are very fine spiral lines between the ribs. The teleoconch is irregularly ribbed; the space between the ribs is greater than on the protoconch. The lip is only slightly thickened and reflexed. There is an elevated, but blunt parietal callus, which has two shallow channels at the meeting point with the lip.

Three specimens were opened. On the parietal wall there is a single curved lamella without any additional plicae. On the palatal wall there are seven horizontal plicae, the first is short and situated near the suture, the last two are divided. The second plica is dichotomously bifurcated posteriorly, and the remaining plicae are more or less parallel with each other.

Differential diagnosis: *Chersaecia laomontana* resembles to *Gudeodiscus* species by the single parietal lamella, rounded body whorl and densely ribbed protoconch. The protoconch of *Ch. laomontana* species however reveals a very unique surface structure, the riblets are comprised of a slight wave and do not stand as regularly as those of *Gudeodiscus*. *Gudeodiscus* species usually have a somewhat elevated spire, more whorls, two horizontal plicae in front of the parietal lamella, and simple (undivided) palatal plicae.

Measurements: (in mm): D= 28.3–32, H= 8.8–9.1 (n=3, syntypes); D= 18.6–21, H= 6.4–7.5 (n=5, specimens from Laos).

Characters of the genital structure: Two specimens were anatomically examined (sample 16L06). The right retractor muscle crosses the penis and vagina.

Penis long, its proximal part is more slender than the dorsal part, internally with 5–6 longitudinal folds standing next to each other; only one of the folds reach the distal end of the penis, the others are shorter; the penis wall (outside of the folded area) is wrinkled; the wrinkles are stronger near the proximal end of the penis; many small, flat, lenticular calcareous granules were found in the penis lumen; epiphallic differentiation was not detected; retractor muscle slightly thinner than the penis and shorter than it; the insertion of the muscle is indicated by a narrowing of both the muscle and the penis; vagina shorter than the half of the penis, the vas deferens forms a part of the vaginal wall and becomes free around the middle of the vagina; it is slender when becomes free, but very slowly thickens to the end; it is the thickest before reaching the spermoviductus; diverticulum short, oval, gametolytic sac with a relatively thick, cylindrical stalk and a thickened, rather quadrangular gametolytic sac; there was a single, well-developed embryo in the uterus.

Radula: Figure 7.98 and Table 7.4.

Distribution: The species was described from "Lao Mountains, Camboja", but exact data on the occurrence of this species in Cambodia are unavailable in the literature or museum collections. I have seen material with more detailed geographical data only from the central part of Northern Laos (around Luang Prabang). In the collection of the Natural History Museum London, a single shell of *Ch. laomontana* is present with the locality "China" (NHMUK 20110363, Salisbury Collection Ex Beddome Ex Canon Hoisley coll. 1918). Its occurrence in China is not verified and the locality is possibly wrong (Figure 7.125).

Remarks: The Type material ("Camboja") are very big (up to 33 mm in width), but the shells from Laos are much smaller (usually less than 21 mm in width).

Sicradiscus Páll-Gergely 2013

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

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

Content: *cutisculptus* (Möllendorff 1882); *diptychia* (Möllendorff 1885); *feheri* Páll-Gergely & Hunyadi 2013; *hirasei* (Pilsbry 1904); *inivius* (Heude 1885); *ishizakii* (Kuroda 1941); *mansuyi* (Gude 1908); *schistoptychia* (Möllendorff 1886); *securus* (Heude 1885); *transitus* Páll-Gergely 2013.

Diagnosis: Shell dextral, very small (5–8 mm), with slightly keeled or rounded body wall; first or first one-and-a-half whorls of the protoconch usually smooth, later regularly, very finely ribbed; there can be periostracum folds on the keel arranged in a spiral line; ventral side of the shell is shiny, occasionally with strong ribs; umbilicus deep and moderately wide; apertural fold is missing or if present, very strong and connected to the callus. Parietal wall with two lamellae, the anterior one always stronger and almost straight, the posterior one weaker, or can be vestigial; palatal plicae short, simple, straight, horizontal to vertical, almost always connected by a ridge, sometimes they are aligned in two rows.

Differential diagnosis: See under *Gudeodiscus* and *Sinicola*.

Etymology: In the Székely dialect of the Hungarian language, the meaning of "szikra" (approximate pronunciation: sicra) is tiny, small. This refers to the small size of species belonging to this genus. The Latin "discus" (= disc, gender masculine) indicates the shape of the shells.

Distribution: Widely distributed from Sichuan and Northern Vietnam to Fujian, Taiwan and Ryukyu Islands (Japan) (Figure 7.127).

Remarks: The genus consists of two species groups, namely (1) *feheri-mansuyi-inivius-securus* possessing a rounded body whorl and strong fold in the aperture, and (2) *cutisculptus-diptychia-ishizakii-hirasei-schistoptychia* with a slightly angulated body whorl and no fold in the aperture. *S. transitus* however, has intermediate shell characters such as an angulated body whorl and a strong apertural fold. The structure of the palatal plicae and the parietal lamellae however, is characteristic of all the species.

***Sicradiscus cutisculptus* (Möllendorff 1882)**

Figures 7.20, 7.50

- 1882 *Plectopylis cutisculpta* Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 9: 184 [type locality not specified].
1883 *Plectopylis cutisculpta*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 10: 375, pl. 12, Fig. 12 ["ad monasterium Yang-hu provinciae sinensis Fudshien"].
1886 *Plectopylis cutisculpta*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 188.
1887 *Helix cutisculpta*, — Tryon, Manual of Conchology, 2 (3): 158, pl. 34, Figs 39–40 [Prov. Fudshien, China].
1896d *Plectopylis cutisculpta*, — Gude, Science Gossip, 3: 180, Figs 26a–c.
1899e *Plectopylis (Sinicola) cutisculpta*, — Gude, Science Gossip, 6: 149.
1899f *Plectopylis (Sinicola) cutisculpta*, — Gude, Science Gossip, 6: 176.
1939 *Plectopylis cutisculpta*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 113, pl. 11, Fig. 21.
2008 *Plectopylis cutisculpta*, — Zhouxing & Deniu, Farmland Molluscs from Zhejiang Province..., p. 243, Figs 125 a–c, 126, p. 383.
2013 *Sicradiscus cutisculptus*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 50, Figs 2 (map), 84 a–b, 103.

Types examined: China: Yang-hu, Fudshien, orig: Yen (1939), pl. 11, Fig. 21, lectotype SMF 9265; China: Yang-hu, Fudshien, Slg. Kobelt, ex Möllendorff, alte Schau-slg., SMF 9266A/6 paralectotypes; China: Yang-hu, Fudshien, Slg. Möllendorff, SMF 9266/13 paralectotypes.

Museum material examined: China: "Hupé". Slg. C. Boschex H. Rolle, SMF 172097/1; Fudshien, coll. Möllendorff, NHMW 40168/26; Fudshien, coll. Möllendorff, NHMW 7216/26; China: Yung-fu, NHMW/2; China, Yungfu, Jorchow district, Hungford, NHMUK 1891.3.17.3535/3; Yung-fu, China, Sow. R., NHMUK 20110359/4; China, Ex Dupuy Ex Kobelt, RBINS/2; China, Yung-pe(?) (probably misspelled Yung-fu), ex coll. Eastlake, J. W., USNM 161707/15.

Diagnosis: A very small, lenticular species with weak apertural rim and callus and fine sculpture. Parietal wall with a strong anterior lamella; second lamella is resorbed into two vertical, vestigial lamellae arranged in a row.

Description: Shell lenticular; yellowish corneous; with 5.5–6 regularly increasing whorls and relatively deep suture; apex smooth, later the protoconch with regular, very finely ribbed sculpture; teleoconch reticulated, with regular, prominent riblets and weaker spiral lines; umbilical side smooth; only widely spaced low growth lines are present; about every 6th–8th dorsal rib continuous towards the umbilicus; inner side of umbilicus has similar sculpture to the dorsal side, but much smoother; umbilicus moderately wide but deep; whorls are rounded ventrally, no keel around the umbilicus; apertural lip thin, only slightly reflected; an inconspicuous callus is present with two low canals at both ends.

Three specimens were opened. Parietal wall with a straight vertical lamella, thickened above and below; posteriorly two small vertical plicae aligned in a row, these are remains of the posterior lamella; palatal side with six plicae, first and second slender and parallel to the sutures; second plica just below the keel; last plica slightly curved or straight, almost parallel with the lower suture; remaining three oblique plicae joined with a ridge.

Differential diagnosis: *Sicradiscus cutisculptus* is larger than *Sicradiscus schistoptychia*, which has a more prominent callus while the parietal plicae are divided in the middle. *Sicradiscus diptychia* is also smaller and has more prominent and a flatter shell. The parietal wall of *Sinicola stenochila* has a curved lamella (the posterior one); the anterior lamella is missing; only few denticles are visible (see also under *stenochila*).

Measurements (in mm): D= 6.5–7.2, H= 3.1–3.4 (n=3, shells from different localities).

Distribution: This species is reported from three localities. The type locality is the monastery of "Yang-hu" (Yanghou Zhen) in Fujian Province. Chen & Gao (1988) as well as Qian et al. (2006) reported the species from Longquan in Southern Zhejiang and some shells from an old collection were collected in Yungfu (Yongfu Temple), which is located in Southern Hunan. The latter locality may be wrong. I was unable to observe the specimens of Chen & Gao (1988) and Qian et al. (2006) (Figure 7.108).

***Sicradiscus diptychia* (Möllendorff 1885)**

Figures 7.20, 7.50

- 1885a *Plectopylis diptychia* Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 12: 390, pl. 10, Fig. 17 ["ad urbem Guiyang provinciae sinensis Gui-dshou"].
- 1886 *Plectopylis diptychia*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 188.
- 1887 *Helix diptychia*, — Tryon, Manual of Conchology...: 158, pl. 34, Figs 46–48 [Prov. Guidshou, China].
- 1898c *Plectopylis diptychia*, — Gude, Science Gossip, 4: 284, Figs 71a–f.
- 1899e *Plectopylis (Sinicola) diptychia*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Sinicola) diptychia*, — Gude, Science Gossip, 6: 176.
- 1920 *Plectopylis (Sinicola) diptychia*, — Gude, Journal of Molluscan Studies, 14 (2–3): 64, Figs 4a–f.
- 1939 *Plectopylis diptychia*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112, pl. 11, Fig. 9.
- 2008 *Plectopylis diptychia*, — Zhouxing & Deniu, Farmland Molluscs from Zhejiang Province..., p. 246, Figs 129 a–c, 130, p. 383.
- 2013 *Sicradiscus diptychia*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 51, Figs 86a–b, 75 (map), 104.

Types examined: Kwei-dshou: China, orig: Yen (1939), pl. 11, Fig. 9. (1), lectotype SMF 9272, SMF 9273/4 paralectotypes with same locality data.

New material examined: Hunan, Zhangjiajie Shi, Zhangjiajie Guojia Senlin Gongyuan, Tianzi Shan Jingqu, near Shuanghedong, 925 m, 29°22.931'N, 110°27.438'E, leg. Hunyadi, A., 24.10.2010, HA/3; Hunan, Zhangjiajie Shi, Wulingyuan Qu, Tianzi Shan, Shuanghedong, 29°22.95'N, 110°27.45'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 9.5.2010, OK/1; Hubei, Zigui Xian, gas station in Shazhenxi Zhen, 198 m, 30°58.28092'N, 110°36.70763'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 12.5.2007, OK/3, PGB/1; Hunan, Huaihua Shi, Huangyan Luyou Dujiaqu, Jinjidong, 876 m, 27°28.300'N, 110°04.109'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 9.3.2009, OK/15, PGB/3.

Diagnosis: A very small, rather flat, keeled species with prominent ribs. Parietal wall with two vertical lamellae.

Description: Shell lenticular, keeled, brownish; consists of 5.25–6 whorls; first whorl of the protoconch smooth; remaining whorls with regularly spaced, extremely fine riblets; teleoconch coarsely ribbed with equally strong spiral sculpture; there can be long deciduous folds on the edge of the whorls (above the keel); on the periphery of the shell there are prominent, irregular, widely spaced ribs; about every 4th–5th dorsal riblet continues on the peripheral surface; these ribs are visible (although weaker) also on the ventral side; umbilicus moderately wide and deep; body whorl rounded around the umbilicus; apertural margin thin, very slightly reflected.

Two specimens were opened. Parietal wall with two vertical lamellae, anterior stronger with its lower part conspicuously thickened; an upper horizontal plica connected with the anterior lamella, which sometimes touches the posterior lamella as well; palatal side with six plicae, first short and situated close to the suture; second long and straight, situated just under the keel; last plica short and slightly oblique; remaining plicae are connected to each other forming a "zigzag" structure.

Differential diagnosis: *Sicradiscus diptychia* can be easily distinguished from its congeners by the prominent, conspicuous ribs. *Sinicola stenochila* is larger, has a more elevated spire and a sharper keel as well as denser ribs on the ventral side. Additionally, *Sin. stenochila* has only one lamella on the parietal wall and some denticles anteriorly.

Measurements (in mm): D= 5.8–6.3, H= 2.8–3.1 (n=3).

Distribution: *Sicradiscus diptychia* was described from Guiyang, Middle Guizhou Province. I have material from the western part of Hunan and Hubei provinces. Yen (1948) reported this species from three localities in Zhejiang Province (Fengshiu, Tunglu, Wongkiang), however I have not seen these specimens (the location of Yen's private collection is unknown) (Figure 7.112).

Remarks: I was unable to examine Yen's specimens (published in Yen 1948) because information regarding the location of Yen's private collection is lacking.

Sicradiscus feheri Páll-Gergely & Hunyadi 2013

Figures 7.21, 7.50

- 2013 *Sicradiscus feheri* Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 52, Figs 58 (map), 82a–b, 106.

Type material: Guangxi, Bose Shi, Lingyun Xian, Lingyun (Sicheng Zhen), Nalingdong, rocks next to the cave, 470 m, 24°21.923'N, 106°33.902'E, leg. Hunyadi, A., 19.10.2009, holotype HHNM 97444, paratypes NHMUK 20120007/1, NHMW 108174/1, SMF 341521/1, HA/19, PGB/7; Guangxi, Hechi Shi, Fengshan Xian, Paoli Xiang,

Poxin, Shuiyuandong (environment of the Lotus Lake), 560 m, 24°24.649'N, 107°01.774'E, leg. Hunyadi, A., 21.10.2009, HA/4; Guangxi, Bose Shi, Lingyun Xian, Xiajia Xiang, SE part of Xiajia, rocky wall above the graves, 440 m, 24°17.508'N, 106°38.376'E, leg. Hunyadi, A., 22.10.2009, HA/1; Guangxi, Lingyun Xian, Baile Gonglu, Xiajia Xiang, 308 m, 24°11.37046'N, 106°36.36007'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 11.7.2006, OK/4, PGB/2; Guangxi, Fengshan Xian, Paoli Xiang, Poxin Shuiyuandong, 567 m, 24°24.66226'N, 107°01.80071'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 14.7.2006, OK/6, PGB/2; Guangxi, Leye Xian, Chuandong, 1088 m, 24°47.98053'N, 106°29.74534'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 13.7.2006, OK/1; Yunnan, Wenshan Zhuangzu Miaozu Zizhizhou, Guangnan Xian, Liji, 1611 m, 23°45.54175'N, 104°59.55567'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.1.2006, OK/1.

Diagnosis: A very small, translucent, shiny *Sicradiscus* species with a strong fold in the aperture. Parietal wall with two thick, vertical lamellae, palatal wall with horizontal plicae.

Description: Shell lenticular, with conical or domed apical part; yellowish/light brown, translucent; 6.25–6.75 whorls separated by rather deep suture; first 1–1.5 whorls of protoconch are smooth; remaining about one whorl is very finely, regularly ribbed; dorsal surface of teleoconch is also finely, but irregularly ribbed; same structure on the upper half of the body whorl; ventral side smooth; umbilicus deep and narrow; apertural margin thickened and strongly reflected; parietal callus elevated and sharp; aperture with a strong fold (denticle) connected to the parietal callus.

Four specimens were opened. Parietal side with two vertical lamellae; first stronger, second also well-developed and can be thick; anterior lamella connected above with a small horizontal plica; another free plica below; palatal wall with five horizontal plicae; first longest and most slender; the four lower, straight and parallel plicae connected by a ridge; last one bit curved posteriorly; an additional vestigial plicula above the first plica is possible to occur.

Differential diagnosis: *Sicradiscus feheri* is closely related to *S. mansuyi*, which was described from Vietnam ("Ha-Lang, Tonkin", not "Ha Long Bay", see Schileyko 2011). The Vietnamese species is smaller, has a more elevated spire making the apical part domed, bears a shallower suture, weaker slightly oblique palatal plicae and the parietal lamellae are less developed (slender). The bigger *Gudeodiscus anceyi* was also described from Vietnam ("Bac-Kan, secteur de Nac-Ri between Cho-Moi and That Khé"). It has a slightly larger aperture than that of *S. feheri*, fine reticulated sculpture on the dorsal side of the shells and the apertural fold is weaker; in some cases it is not connected to the callus.

There are three Chinese species, which resemble *S. feheri*: *S. inuius*, *S. securus* and *S. transitus*. *S. inuius* is smaller than *S. feheri*, and has shorter, oblique palatal plicae. On the other hand, *S. securus* is slightly bigger, has a deeper umbilicus, its palatal plicae are oblique and connected by a continuous ridge. There is probably only one lamella on the parietal wall. *S. transitus* has a slightly keeled body whorl, widely-spaced ribs on the ventral side of fresh shells, and palatal plicae aligned in two rows, or aligned in one row with the penultimate plica vertically positioned.

Measurements (in mm): D= 7.3–8.0, H= 3.6–4.4 (n=4, shells from different localities).

Etymology: This species is dedicated to my friend, Zoltán Fehér (HNHM) in acknowledgement of his boundless help throughout my studies.

Type locality: Guangxi, Bose Shi, Lingyun Xian, Lingyun (Sicheng Zhen), Nalingdong, rocks next to the cave, 470 m, 24°21.923'N, 106°33.902'E.

Distribution: *Sicradiscus feheri* is known from Eastern Yunnan and western part of Guangxi (Figure 7.110).

***Sicradiscus hirasei* (Pilsbry 1904)**

Figures 7.22, 7.50

1904 *Plectopylis (Sinicola) hirasei* Pilsbry, Nautilus, 18: 58–59. ["Miyakojima, Riukiu"]

1963 *Plectopylis hirasei* Baker, Proceedings of the Academy of Natural Sciences of Philadelphia 115 (8): 215.

1984 *Plectopylis (Sinicola) hirasei*, — Azuma & Azuma, Satuki, 20: 89–90.

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

Types: Miyakoshima, Loochoo, leg. Hirase '04, ANSP 87632 (lectotype, selected by Baker 1963, image received from Francisco Borrero); same data, ANSP 457396 (3 paralectotypes) (not examined).

Museum material examined: Loo Choo: Miyakoshima, coll. Dosch ex Rolle, SMF 172109/2; Miyakejima, Loo Choo Ids, NHMUK 1905.2.22.4–5/2; Miyaki-shima, Loo Choo Is., NHMUK 1920.1.20.20/1; Loo Choo Id, 13/12/04, NHMUK/3.

New material examined: Mt. Nobaru, Miyako Island, Okinawa, Japan, leg. Minato, H., 22.03.1979., PGB/5.

Measurements (in mm): D= 5.95–6, H= 2.95–3.05 (n=3, new material).

Diagnosis: A *Sicradiscus* species with domed dorsal side, and ribbed (not glossy) ventral side, strong callus without apertural fold and simple palatal plicae.

Description: Shell lenticular, brownish, spire elevated resulting in a domed dorsal surface; protoconch consists of 2.25–2.5 (n= 3) whorls, very finely, regularly ribbed; teleoconch finely reticulated on both dorsal and ventral sides; on the dorsal side the radial and spiral lines are of the same strength, on the ventral side the radial sculpture is stronger; periostracal folds may present, but I had only corroded shell for examination; body whorl bluntly shouldered; the 5.5–5.75 (n=3) whorls are separated by relatively shallow suture; umbilicus relatively narrow and deep; peristome slightly thickened and reflexed, callus very much elevated, rather blunt, angled in its middle, at both ends there are deep channels at the meeting points with the peristome.

Two specimens were opened; anterior lamella well-developed, curved, thickest at its lower end, slightly C-shaped, with the arms of the C pointing in posterior direction; the upper end of the anterior lamella elongated anteriorly and posteriorly as well; posterior lamella vestigial, abruptly in the middle, its upper end is connected to the posterior elongation of the anterior lamella; palatal plicae 6, the first and 6th very slender, short, the second relatively long, the remaining ones thick and oblique.

Differential diagnosis: For comparisons with *S. ishizakii* see under that species. *S. hirasei* differs from the "eastern *Sicradiscus*" taxa (*S. diptychia*, *S. cutisculptus*, *S. schistoptychia*) by the non-glossy ventral side. The remaining ("western") species of the genus possess a strong apertural fold.

Distribution: The species is known only from Miyako Island, Okinawa.

Sicradiscus invius (Heude 1885)

Figures 7.21, 7.50, 7.81, 7.92, 7.103

1885 *Helix invia* Heude, 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, 111, pl. 30, Fig. 4 ["Tchen K'eu"].

1886 *Plectopylis invia*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 189.

1887 *Helix invia*, — Tryon, Manual of Conchology, 2 (3): 165, pl. 36, Figs 17–20 [Tchenkeou, China].

1896d *Plectopylis invia*, — Gude, Science Gossip, 3: 181, Figs 28a–b.

1897a *Plectopylis invia*, — Gude, Science Gossip, 3: 204.

1899e *Plectopylis (Sinicola) invia*, — Gude, Science Gossip, 6: 149.

1899f *Plectopylis (Sinicola) invia*, — Gude, Science Gossip, 6: 176.

1939 *Plectopylis invisa* (sic!), — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 113, pl. 11, Fig. 20.

2013 *Sicradiscus invius*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 52, Figs 59 (map), 83a–b, 108–109.

2014a *Sicradiscus invius*, — Páll-Gergely & Asami, Genus 25(3): 541, Figs 13, 21A.

Types examined: "Tchen-k'eu", syntype USNM 472167.

Museum material examined: China: Hubei, Slg. O. Möllendorff, SMF 42727/5+1; China: Prov. Hubei, Slg. O. Boettger ex V. Gredler, 1888, SMF 42728/3; China: Hunan, Slg. C. Boschex H. Rolle, SMF 172102/2; China: Prov. Hubei, Slg. C. R. Boettger, 1906, SMF 118086/9; China: Hubei, Slg. Jetschin 1928 ex Möllendorff, SMF 11808/2; Hubei, Coll. Möllendorff, NHMW 40176/19; Hubei, ex coll. Möllendorff, NHMW 7217/2; Hupé, China, NHMUK 1916.3.16.8/1; Hupé, NHMUK 20110360/1; Heupe, China '99, NHMUK 20110361/1; Chine, Coll. Letellier, 1949, MNHN/1; Hupé (Chine), Schneider 29.11.91., RBINS/2; China, Hupé, ex coll. Dr. Brancsik, NHMSB, 131/197, 122803–122804 (2 specimens); China, Hu-bei, ex coll. Möllendorff, USNM 184697/2; China, Hupé, ex coll. Rolle, USNM 110169/2.

New material examined: 20070708B Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghou Shan, Sanlong Shuijingrongdong, 942 m, 30°55.15418'N, 103°29.72375'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 8.7.2007, HA/1, OK/6, PGB/2; Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghou Shan, Cuiyinghu to upper Jinli cable station, 1273 m, 30°56.27110'N, 103°28.75198'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.7.2007, OK/2; Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghou Shan, above the lower Jinli cable station, 979 m, 30°55.62540'N, 103°29.08667'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 8.7.2007, OK/5; Sichuan, Dujiangyan Shi, Qingchengshan Zhen, below Woyunsi, 1110 m, 30°54.33919'N, 103°33.40153'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 10.7.2007, OK/1.

Diagnosis: A very small, translucent *Sicradiscus* species with a strong fold in the aperture. Parietal wall with two vertical lamellae; palatal wall with vertical or oblique middle plicae.

Description: Shell depressed-conical; translucent; yellowish; teleoconch very finely, irregularly ribbed on the dorsal side; smooth at the bottom and on the periphery; whorls six, suture rather deep; umbilicus deep and narrow; apertural margins thickened and strongly reflected; parietal callus elevated and sharp; aperture with strong fold, connected to the parietal callus.

Three specimens were opened. Parietal wall with two vertical lamellae; anterior one much stronger; posterior very slender, or even totally reduced or missing in some cases; anterior lamella connected above and below with two small horizontal plicae; first (the longest) and last palatal plicae are thin and horizontal; second thick; third and fourth plicae oblique or almost vertical; connected by a callous ridge to each other.

Differential diagnosis: *S. invius* resembles *S. feheri*, which is larger, has stronger sculpture and all the palatal plicae are horizontal. *Sic. securus* is also bigger, has a deeper umbilicus and only a single lamella on the parietal wall. Similar species inhabit Vietnam (*anceyi*, *mansuyi*). See under *S. invius*.

Measurements (in mm): D= 6.5–6.6, H= 3.2–3.4 (n=2).

Characters of the genital structure: Two specimens were anatomically examined. Ethanol-preserved bodies are deposited in coll. PGB, respective shells in coll. JUO. Locality information: **20130917A** Sichuan, Dujiangyan Shi, Taian Zhen, Sanlong Shuijingrongdong, 1087 m, 30°55.039'N, 103°29.662'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 17.09.2013.

The right ommatophoral retractor crosses the male and female genitalia. Penis short, blunt, consists of a longer proximal and a shorter distal portions; it is the widest at the distal end of the proximal part; inner wall with rather parallel folds which form "pockets" in the distal part of the penis; penial caecum missing, epiphallus is a little longer than the distal part of the penis; the extremely long retractor muscle attaches to the point of penis-epiphallus transition; Vagina longer than the penis, with well-developed vaginal bulb and many short fibres which connect it to the diaphragm; vas deferens slender, but thickened at the end; additional organ next to the gametolytic sac slender, long; gametolytic sac slightly shorter and tapers towards the end.

Radula: Figure 7.103 and Table 7.4.

Distribution: This species was described from "Tchen K'ou" (Chengkou). Most of the museum material is from Hunan and Hubei. I have examined material only from Middle Sichuan, where it sometimes occurs together with *S. murata* (Figure 7.111).

Sicradiscus ishizakii (Kuroda 1941)

Figures 7.22, 7.50

1941 *Plectopylis (Sinicola) ishizakii* Kuroda, Memoirs of the Faculty of Science and Agriculture, Taihoku Imperial University, 22: 142, 188–189, Plate 7, Figs 42–43. ["Tentana, Tikutō, Sintiku-syū"].

1999 *Plectopylis (Sinicola) ishizakii*, — Chang & Ookubo, Bulletin of Malacology, Taiwan ROC, 23: 21–23, Figs 1–2, 3-1, Plate 1, Figs 1–3, ["Hsiau-urai"]

2008 *Plectopylis ishizakii*, — Hwang, Wu, Ohara, Otani & Otani, Venus 67 (1–2): 58, Fig. 5.

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

Types: Tentana, Tikutō, Sintiku-syū, leg. Kuroda, 30.04.1939., NCP 244 (paratype).

New material examined: Taiwan, BaLing, Tao Yuang Xian, leg. Okubo, K., 16.05.1993., PGB/2.

Diagnosis: A *Sicradiscus* species with only slightly elevated spire, glossy base with widely-spaced, irregular ribs, strong callus without apertural fold, and simple palatal plicae.

Description: Shell depressed-conical; translucent; brownish; protoconch consists of 2.25 whorls (n=2), very finely ribbed; teleoconch finely reticulated on the dorsal side; sculpture dominated by radial sculpture; long flat periostracal filaments visible in fresh shells; the filaments are present on approx. every 5th ribs; ventral side glossy, with widely-spaced, irregular, low radial lines; 5–5.25 whorls (n=2) are separated by rather deep suture; body whorl shouldered; umbilicus deep and relatively narrow, with reticulated sculpture inside; peristome slightly thickened and reflexed; callus sharp, elevated, very slightly S-shaped, with shallow channels at both ends at the meeting points of the peristome.

Two specimens were opened. The anterior lamella well-developed, slightly C-shaped with the arms of the C pointing in posterior direction; the lower part of the lamella is much thicker than the upper part, and it becomes gradually slimmer in upper direction; the posterior lamella is vestigial, its lower end is thin, its middle part is nearly not visible, and its upper oblique or almost horizontal end is connected to the upper end of the anterior lamella in one

specimen and not connected in the other. Palatal plicae six, the first is very slim and short, situated close to the suture, the last is thicker than the first, curved, situated in some distance from the lower suture; second plica the longest, relatively straight, situated just above the "keel"; 3rd–5th plicae short, thick, oblique.

Differential diagnosis: *S. ishizakii* differs from *S. hirasei* by the flatter shell and glossy base, from *S. schistoptychia* by the simple palatal plicae, and by *S. diptychia* by the weaker radial ribs and stronger callus. *S. cutisculptus* also much weaker callus. *S. invius*, *S. securus*, *S. manusuyi*, *S. feheri* and *S. transitus* all possess a well-developed apertural fold.

Measurements (in mm): D= 5.9–6.15, H= 2.9–3 (n=2, new material).

Distribution: *S. ishizakii* is reported from a few Taiwanese localities only.

***Sicradiscus manusuyi* (Gude 1908)**

Figures 7.22, 7.42, 7.82, 7.103

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

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

2015 *Sicradiscus manusuyi*, — Páll-Gergely et al., Zookeys 472: 86, Figs 2A, 9H, 11A–B, 27, 31A, 36J–L.

Types examined: Tonkin, Ha-Lang, leg. Mansuy, NHMUK 1907.2.20.19 (syntype).

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 Rào Village, 544 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 Rào, 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/9+5 jb; **2012/44** Cao Bằng Province, southern edge of Pắc Rào, 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 Đông Vãn, 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 Giang Province, km 105.5 on road 4c, between Yên Minh and Đông Vãn (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 Đông Vãn (NE of Hà Giang town), no GPS-data, leg. Hemmen, Ch., 22.03.2011., HE/3; **20050327A** China, Guangxi, Daxin Xian, Xialei Zhen, Detianpubu, Detian waterfalls, leg. Ohara, K. & Moriya Shigeki, 27.03.2005., PGB/1.

Diagnosis: A very small species with reticulated dorsal and shiny ventral surface, elevated spire, elevated, sharp callus and well-developed apertural fold connected to the callus. Parietal wall with two lamellae, the anterior one is separated from both the lower and upper plicae; middle palatal plicae short, connected with a ridge and ornamented with small denticles posteriorly.

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 longer, horizontal palatal plicae without additional posterior denticles, and has a more elevated and longer apertural fold. *S. 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. manusuyi*. *S. invius* is flatter (has shallower umbilicus) with only the protoconch elevated from the dorsal surface; it has weaker dorsal sculpture resulting in a shiny surface (*mansuyi* is densely reticulated), and lacks the additional small denticles posterior to the palatal plicae, which are present in *S. manusuyi*. *Gudeodiscus anceyi* is larger and has a ribbed shell with spiral lines on the whole shell. Species possessing a shiny ventral surface (*G. cyrtochilus*, *G. fischeri*) are also larger and have weaker or lack an apertural fold.

Measurements (in mm): D= 6.7–7, H= 3.4–3.9 (n=4, 2008.11.16C).

Characters of the genital structure: Two specimens were anatomically examined (Cao Bằng Province, southern edge of Pắc Rào, 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.

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 & Asami 2014); these “pockets” did not contain granules; epiphallus approximately as long as the penis but much slimmer; internally penis and epiphallus wall with longitudinal, 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; vas deferens long, thicker distally and more slender proximally; gametolytic sac and diverticulum are of equal length, in parallel.

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

Radula: Figure 7.103 and Table 7.4.

Distribution: This species was described from Hà Lang (eastern part of Cao Bằng Province). I have seen newly collected material from northern Hà Giang and Cao Bằng provinces. I also report the first occurrence of the species from China. This locality is situated very close to the Vietnamese border (Figure 7.115).

***Sicradiscus schistoptychia* (Möllendorff 1886)**

Figures 7.21, 7.31, 7.50, 7.83, 7.103

1886 *Plectopylis schistoptychia* Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 185, pl. 6, Fig. 2 [In provinciae sinensis Hunan parte meridionali].

1887 *Helix schistoptychia*, — Tryon, Manual of Conchology, 2 (3): 165, pl. 36, Figs 21–22 [Prov. Hunan, China].

1897i *Plectopylis schistoptychia*, — Gude, Science Gossip, 4: 102–103, Figs 56a–e.

1899e *Plectopylis (Sinicola) schistoptychia*, — Gude, Science Gossip, 6: 149.

1899f *Plectopylis (Sinicola) schistoptychia*, — Gude, Science Gossip, 6: 176.

1920 *Plectopylis (Sinicola) schistoptychia*, — Gude, Journal of Molluscan Studies, 14 (2–3): 64, Figs 3a–e.

1939 *Plectopylis schistoptychia*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 113, pl. 11, Fig. 19.

2013 *Sicradiscus schistoptychia*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 53, Figs 75 (map), 85a–b, 92, 105, 115.

2014a *Sicradiscus schistoptychia*, — Páll-Gergely & Asami, Genus 25(3): 541–542.

Types examined: China: Hunan, Heng-shan-shien, Slg. Möllendorff, lectotype SMF 9263, SMF 9264a/6 paralectotypes; China: Hunan, Heng-shan-shien, Slg. O. Boettger ex Möllendorff, SMF 9264b/4 paralectotypes.

Museum material examined: China: Hunan, Heng-shan-shien, Slg. Möllendorff, NHMW 40192/12; Hunan: Heng-shan-shien ex coll. Möllendorff, NHMW 7144/2; Hunan, Hungerford, NHMUK 91.3.17.360.1/2.

New material examined: Hubei, Yichang Shi, Sanyoudong, Yichang NNW, 80 m, 30°46.035'N, 111°15.752'E, leg. Hunyadi, A., 29.10.2010, HA/4; **2010/48** Hunan, Yongzhou Shi, Ningyuan Xian, Jiuyishan Yaozu Xiang N Jiuyishan Guojia Senlin Gongyuan, old maple forest, 450 m, 25°21.200'N, 111°58.696'E, leg. Hunyadi, A., 11.11.2010, SMF 341522/1, HA/56, PGB/4; Hunan, Yongzhou Shi, Ningyuan Xian, Ningyuan N 2 km, Xiabeitang NE, northern slope of the mountain, around the cave, 230 m, 25°37.045'N, 111°58.206'E, leg. Hunyadi, A., 10.11.2010, HA/38; Hunan, Yongzhou Shi, Ningyuan Xian, Ningyuan NW 2,5 km, eastern edge of Xiaoyaoyan Cun, isolated rock, 225 m, 25°37.268'N, 111°57.714'E, leg. Hunyadi, A., 10.11.2010, HA/1.

Diagnosis: A very small, lenticular species with elevated, sharp callus. Palatal plicae are separated in the middle.

Description: Shell lenticular; brownish or corneous; consists of 5.5–6, slowly increasing whorls, separated by a rather deep suture; first whorl of the protoconch smooth; the remaining whorl very finely ribbed; teleoconch ribbed with spiral contours, resulting in an overall reticulated dorsal surface structure; ventral side with irregular growth lines only; umbilicus very deep, moderately wide; apertural rim thickened and slightly reflected; a prominent, sharp callus continuous with the apertural lip, whereby at both ends of the callus shallow canals are visible; an inconspicuous small denticle may be present in the aperture just behind the callus.

Five specimens were opened. Parietal wall with two vertical lamellae, anterior one much stronger, posterior one slimmer and lower; the lower part of the anterior lamella thickened and on the upper side, joins to a horizontal plica; palatal side with two normal plicae, first very small, hardly visible; second slender and very long, runs just below the keel; third to sixth plicae divided; anterior section of the plicae with short, denticle-like structures aligned in a row, posterior plicae obliquely elongated.

Differential diagnosis: The sharp callus and the divided palatal plicae make the determination of this species easy.

Measurements (in mm): D= 6.2–6.7, H= 3.1–3.2 (n=3, shells from different localities).

Characters of the genital structure: One specimen was dissected. The right ommatophoral retractor crosses the genitalia. Within the uterus two well-developed embryos were found with a calcium-free protoconch. Their embryo sac however, contained several tiny calcareous crystals.

Penis very long and slim, more than two times longer than the epiphallus; inner wall of the posterior half of the penis contained approximately 12 simple parallel folds with tiny calcareous crystals between them; I found no signs of characteristic "pockets" (see under *Gudeodiscus* species, *Sic. invius* and *Sic. transitus*); the proximal, extremely slender half of the penis had smooth internal wall.; penial caecum about as long as the epiphallus; retractor muscle attaches to the end of the penial caecum; vagina slightly shorter than the penis, has a swelling at about mid section; no attaching filaments were found on the vagina; gametolytic sac and an additional organ are very long and slim.

Radula: Figure 7.103 and Table 7.4.

Distribution: This species is known from Hunan and Hubei Provinces. Hu et al. (2004) reported the species from Nanling Guojia Gongyuan (National Park), Northern Guangdong. This record could not be verified by us (Figure 7.112).

Remarks: My observations on the parietal lamellae do not corroborate with Gude's (1897i) drawing (page 103, Fig. 56e), designating a single lamella with a dichotomously divided lower end. According to Gude (1897i) the figured specimen is "in the collection of Professor Boettger, of Frankfurt". In the collection of the SMF there is a sample of *S. schistoptychia* from the collection of O. Boettger (SMF 9264B/4), but these specimens were intact. I have not found any shells in Gude's collection with a structure identical to his drawing. I assume that Gude did not observe the parietal lamellae, but published a drawing, which explains the name "schistoptychia" (Greek: "divided lamella"). See also in Chapter 8 (Figure 8.3).

Sicradiscus securus (Heude 1889)

Figures 7.21, 7.50

1889b *Helix securus* Heude, Journal de Conchyliologie, 37: 226 [Kouang Si].

1890 *Helix securus*, — Heude, 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, 4: 141, pl. 38, Figs 6, 6a [Si Lin (Kouang-si)].

1898a *Plectopylis securus*, — Gude, Science Gossip, 4: 231, Figs 65a–d.

1899e *Plectopylis (Sinicola) securus*, — Gude, Science Gossip, 6: 149.

1899f *Plectopylis (Sinicola) securus*, — Gude, Science Gossip, 6: 176.

2013 *Sicradiscus schistoptychia*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 55, Figs 2 (map), 87, 110.

Types examined: Si-lin, Kouang-si, 1889, ex coll. Musée Heude, Shanghai, China, acc. 1253, syntype MCZ 167129.

Diagnosis: A very small, shiny *Sicradiscus* species, with a small fold in the aperture connected to the low callus, oblique palatal plicae connected by a ridge, one single lamella on the parietal wall.

Description: Shell white/light grey; discoid with slightly, conically elevated spire; finely striated above; glossy below; umbilicus relatively narrow; there are 6.5 regularly growing whorls; aperture relatively wide; apertural rim slim and reflected; its margins are joined by a low callus; and there is a weak apertural horizontal fold.

Parietal wall with possibly a single vertical plate, which appears to be straight; on the palatal wall there are six plicae; the first is very weak and borders the suture; the others are oblique except the vestigial last one; second plica is the longest and is not connected to the others; the third, fourth and fifth plicae are connected by a ridge.

Differential diagnosis: The species is larger than *Sic. invius* and *Sic. feheri*, has deeper umbilicus and probably only a single lamella on the parietal wall.

Measurements (in mm): D= 8.5, H= 4.4 (syntype).

Distribution: The species is known only from Xilin, Guangxi (Figure 7.108).

Remarks: I have only viewed a single specimen (MCZ 167129). Therefore the variability within the species is not known. The parietal wall could only be observed through the shell of the body whorl, without breaking a window through the surface in order to view it. As far as could be seen however, the observed specimen had only one lamella on the parietal wall, which corroborates with Heude's (1890) drawing.

Sicradiscus transitus Páll-Gergely 2013

2013 *Sicradiscus transitus* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 55, Figs 58 (map), 88a–c, 107.

2014a *Sicradiscus transitus*, — Páll-Gergely & Asami, Genus 25(3): 542–544, Figs 14, 21B.

Type material: Guangxi, Nandan Xian, Lihuyaozu Xiang, En Cun, Ganendong, 579 m, 25°04.270'N, 107°36.102'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 20.10.2011, holotype HNHM 97485, paratypes NHMW 108171/1, NHMUK 20120004/1, SMF 341523/1, HA/1, OK/16, PGB/10; Guangxi, Nandan Xian, Lihuyaozu Xiang, En Cun, 614 m, 25°03.355'N, 107°36.280'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 20.10.2011, OK/3, PGB/1; Guangxi, Tiane Xian, Qimu Xiang, Duloulieshita, 602 m, 24°51.114'N, 107°11.666'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 21.10.2011, OK/4, PGB/2; Guangxi, Huanjiangmaonanzu Zizhixian, Dacai Xiang, Nongmaoshi Chang, 201 m, 24°45.566'N, 108°21.945'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 19.10.2011, OK/1; Guangxi, Huanjiangmaonanzu Zizhixian, southwest Sien Zhen, 306 m, 24°46.525'N, 108°16.978'E, leg. Ishibe, T., Ohara, K., Okubo, K. & Otani, J. U., 19.10.2011, OK/1 juvenile, not paratype; Guangxi, S-edge of Maolan Nature Reserve, at the border with Guizhou, S of Libo, leg. Whitten, T. September 2004, ex coll. Maassen, W., PGB/1, WM/9 adults (paratypes) and 10 juveniles (not paratypes).

Diagnosis: A very small, slightly keeled species with strong callus and widely spaced riblets on the ventral side of the shell. Palatal plicae stand in two lines or in one line; in the latter case the penultimate plica is vertical.

Description: Shell light brown, off-white or corneous; body whorl angled with slight upper keel; dorsal side finely reticulated; ventral surface distantly ribbed, but some shells lost these ribs due corrosion; apertural rim slightly thickened and reflected, callus very well-developed, elevated and sharp; the relatively weak apertural fold in contact with the callus.

Three specimens were opened belonging to different populations. Parietal wall with two lamellae, posterior very weak, just slightly indicated; anterior high, connected with short and slim horizontal plicae above and below; palatal plicae can comprise a single line or can be divided (this character has no diagnostic value). The shells from Duloulieshita and En Cun had only divided plicae, whereas in the sample from Ganendong, specimens revealed normal as well as divided plicae.

Differential diagnosis: *Sicradiscus transitus* is a bit smaller than *S. feheri*, it usually has a more elevated callus and a slimmer apertural fold, its body whorl is slightly angulate, and fresh specimens are ribbed on the ventral side. The palatal plicae are also different. They can either stand in a line and the penultimate is vertical or the plicae can be divided into two lines. The Vietnamese *S. mansuyi* has a more elevated spire, rounded body whorl and much weaker, oblique palatal plicae.

Measurements (in mm): D= 5.9–6.7, H= 3.0–3.4 (n=4, shells from different localities).

Characters of the genital structure: Two subadult specimens (without "finished" peristome) were anatomically examined (stored in coll. PGB). The locality data are the following: **2013/8** 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.

The right ommatophoral retractor crosses the male and female genitalia. Shell and genital organs were immature. Penis rather long, consists of slim proximal and thick distal portions which are approximately the same in length; the width of the penis changes gradually between the two portions; distal end of penis with very small penial caecum-like part; long retractor muscle attaches the caecum; epiphallus about as long as the distal, thickened part of the penis; inner wall of the penis with approximately 10 parallel folds which are becoming more pronounced towards the distal end of the penis, where the folds are more elevated and form "pockets". Very tiny calcareous crystals were found between these "pockets". Vagina also long, with well-developed vaginal bulb; with several short fibres attaching it to the diaphragm.

Radula: Figure 7.104 and Table 7.4.

Etymology: This species merits this name because it connects the "*invius*-group" (*feheri-invius-mansuyi-securus*) and the "*cutisculptus*-group" (*cutisculptus-diptychia-hirasei-ishizakii-schistoptychia*) by having intermediate shell characters (see under *Sicradiscus*).

Type locality: Guangxi, Nandan Xian, Lihuyaozu Xiang, En Cun, Ganendong, 579 m, 25°04.270'N, 107°36.102'E.

Distribution: *Sicradiscus transitus* is known only from a small area in Northern Guangxi (Figure 7.110).

Remarks: A subadult specimen from Duloulieshita had short hairs standing in two lines on the body whorl; one line just below the keel and the other is slightly under the middle line of the body whorl. Hairs standing in multiple (usually 3–5) lines were known only in the genus *Endothyrella*.

Genus *Sinicola* Gude 1899

1899e *Sinicola* Gude (section of *Plectopylis*), Science Gossip, 6: 148.

Type species: *Helix fimbriosa* von Martens 1875, by original designation.

Content: *asamiana* Páll-Gergely 2013, *biforis* (Heude 1885), *emoriens* (Gredler 1881), *fimbriosa* (Martens, 1875), *jugatoria* (Ancey 1885), *murata* (Heude 1885), *reserata* (Heude 1885), *azona* (Gredler 1887), *schmackeri* Páll-Gergely 2013, *stenochila* (Möllendorff, 1885), *stenomphala* Páll-Gergely & Hunyadi 2013, *straeleni* (Yen 1937), *vargabalinti* Páll-Gergely 2014.

Taxa with unknown identity: *alphonsi* (Deshayes 1870), *hensanensis* (Yen 1939), *vallata* (Heude 1889), *emoriens* var. *nana* (Möllendorff 1886), *fimbriosa* var. *hunanica* (Schmacker & Boettger 1890).

Diagnosis: Shell dextral, flat or with domed apical region, body whorl angulated, usually with deciduous periostracal folds; protoconch very finely, regularly ribbed; rougher sculpturing of the dorsal region of the teleoconch changes to a moderately prominent sculpture under the keel; umbilicus moderate or wide; apertural fold very rare; missing in almost all species (only exception is *S. biforis*); palatal plicae usually simple, parallel and horizontal; parietal wall with a single horizontal lamella and two horizontal plicae anterior of the lamella, one above, and one below, close to the sutures; between these plicae there can be 1–4 short denticles.

Differential diagnosis: *Sicradiscus* species differ from *Sinicola* species by the strong anterior parietal lamella which is missing in *Sinicola* or is dissolved into small denticles. Moreover, western *Sicradiscus* species have rounded body whorl with strong fold in the aperture. *Gudeodiscus* species also has rounded body whorl. Moreover, *Gudeodiscus* has characteristic pockets formed by the parallel folds on the inner penial wall, standing in one or two rows. These are absent in *Sinicola* which has only parallel folds.

Distribution: China (Northern Guangxi-Jiangxi-Middle Hubei-Middle Sichuan) (Figure 7.127).

Remarks: If the deciduous folds are not mentioned in the description, it can be the result of old, corroded shells.

Sinicola alphonsi (Deshayes 1870)

Figure 7.19

1870 *Helix alphonsi* Deshayes, Bulletin des Nouvelles archives du Muséum d'Histoire Naturelle. 6: 22.

1873 *Helix alphonsi*, — Deshayes, Bulletin des Nouvelles archives du Muséum d'Histoire Naturelle. 9: 13, pl. 2, Figs 22–24.

1895 *Eulota alphonsi*, — Pilsbry, Manual of Conchology, 2 (9): 211.

1899a *Plectopylis alphonsi*, — Gude, Science Gossip, 5: 239, Fig. 94.

1899e *Plectopylis (Sinicola) alphonsi*, — Gude, Science Gossip, 6: 149.

1899f *Plectopylis (Sinicola) alphonsi*, — Gude, Science Gossip, 6: 176.

1902 *Plectopylis alphonsi*, — Möllendorff, Binnen-Mollusken aus Westchina und Central-Asien II.. 10 (308).

2013 *Sinicola alphonsi*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 34, Figs 2 (map), 70.

Types examined: "Monpin, Thibet Oriental", syntype (holotype?) MNHN 24717.

Diagnosis: A small species with low but sharp callus. Palatal plicae obliquely parallel with each other and connected by a ridge.

Description: Shell yellowish; lenticular; consists of 6 whorls which are separated by a relatively shallow suture; teleoconch irregularly, roughly ribbed; ribs decussated by spiral lines; ventrally, only irregular growth lines are visible; umbilicus deep and moderately wide; apertural rim only slightly thickened; callus sharp, but low, S-shaped; a hint of an apertural fold is present.

Palatal wall with six straight plicae; second-fifth plicae connected by a callous ridge. Unfortunately the parietal lamellation could not be observed.

Differential diagnosis: The type specimen most resembles *S. reserata*. Further material is necessary for a detailed differential diagnosis.

Measurements (in mm): D= 9.1, H= 4.1 (syntype).

Distribution: The species was recorded from the type locality only. See Remarks and Figure 7.108.

Remarks: The locality of *Sin. alphonsi* may be wrong. Möllendorff (1902) also concluded this. The known relatives of *Sin. alphonsi* are recorded from Middle Sichuan and east of this region (Hunan, Hubei, Chongqing, Guizhou, north-eastern Guangxi). The same problem arose for the case of the clausiliid *Synprosphyra tibetiana* (Deshayes

1870). It was described in the same publication and from the same locality as *Sin. alphonsi*. Nordsieck (2001) however, mentioned *Syn. tibetiana* from Sichuan together with its close relatives from the same province. Gude received a shell from Gredler from Kouei-Tchou (Guizhou Province), which was identical to *S. alphonsi* (Gude 1899a). In the Natural History Museum, London (among Gude's samples), I could not find this specimen. Until further examination of the parietal plicae and lamellae and the availability of more material can be accomplished, the identity of this species remains doubtful.

***Sinicola asamiana* Páll-Gergely 2013**

Figures 7.20, 7.50, 7.84, 7.92, 7.104

2013 *Sinicola asamiana* Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 34, Figs 93 (map), 101.

2014a *Sinicola asamiana*, — Páll-Gergely & Asami, Genus 25(3): 544, Figs 15, 21C.

Type material: Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghou Shan, Shenxiandong, 835 m, 30°54.61750'N, 103°30.97445'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.7.2007, holotype HNHM 97452, paratypes OK/3, PGB/1; Tchen-K'eou, China, ex coll. Musée Heude, Shanghai, China (Acc.1253), MCZ 374360/1 ex *reserata*; Sichuan, Dujiangyan Shi, Qingchengshan Zhen, Qingchengshan Shangqinggong, 1165 m, 30°54.77004'N, 103°33.70697'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 10.7.2007, OK/2, PGB/1; Sichuan, Emeishan Shi, Qingyinge, Eshan Zhen, Emeishan, 752 m, 29°34.59132'N, 103°23.57642'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 14.7.2007, HA/1, OK/2; Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghou Shan, Shengmudong, 763 m, 30°52.79850'N, 103°33.24453'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.7.2007, OK/1.

Additional material: 20130917A Sichuan, Dujiangyan Shi, Taian Zhen, Sanlongshuijingrongdong, 1087 m, 30°55.039'N, 103°29.662'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., JUO/1; Sichuan, Dujiangyan Shi, Qingchengshan Zhen, Jinbianyan, 860 m, 30°53.762'N, 103°33.101'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 16.09.2013.

Diagnosis: A very small, brown *Sinicola*, with an elevated parietal callus and small denticles between the two horizontal lamellae in front of the vertical lamella on the parietal wall.

Description: Shell lenticular, brownish; the few available shells are corroded while the periostracum is lacking from the majority of the dorsal surface; the 5.25–6 regularly expanding whorls are separated by a shallow suture; teleoconch very finely ribbed and the surface is reticulated due to spiral striae; spiral structure much weaker on the ventral side; umbilicus deep and narrow; aperture lip conspicuously thickened and reflected; parietal callus prominent, elevated, with shallow canals at both ends.

Two specimens were opened. Parietal wall with one vertical, curved lamella and four small denticles preceding it (anteriorly); palatal wall with six short horizontal or slightly oblique plicae.

Differential diagnosis: *S. jugatoria* is much larger, has a wider umbilicus, has a thinner apertural lip and has only two short plicae anterior to the vertical lamella (one above and one below, near the sutures). *S. reserata reserata* is about twice as large, has a wider umbilicus and a weaker callus.

Measurements (in mm): D= 7.7–9.6, H= 4.0–5.0 (n=3, shells from different localities).

Characters of the genital structure: One specimen was dissected. Ethanol-preserved body is deposited in coll. PGB, respective shell in coll. JUO. Locality information: Sichuan, Dujiangyan Shi, Qingchengshan Zhen, Jinbianyan, 860 m, 30°53.762'N, 103°33.101'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 16.09.2013.

The right ommatophoral retractor crosses the male and female genitalia. Penis very long, rather flat, equally wide to the end, internally with approximately 10 parallel, longitudinal folds; penial caecum as wide as penis; penis about five times as long as the penial caecum; epiphallus as long as the caecum but much thinner, spindle-shaped than the caecum; retractor muscle attaches the distal end of the penial caecum, and is extremely slender and almost four times as long as the penis. Vagina flat, almost twice as long as the penis and much thicker than the penis; no vaginal bulb present; vagina attached to the diaphragm with a few long and widely-spaced fibres; proximal part of vas deferens slender but distal end thickened; gametolytic sac and the additional organ next to the gametolytic sac are both very slender and extremely long.

Radula: Figure 7.104 and Table 7.4.

Etymology: This species is dedicated to and named after my supervisor, Takahiro Asami.

Type locality: Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghou Shan, Shenxiandong, 835 m, 30°54.61750'N, 103°30.97445'E.

Distribution: The species is known only from middle Sichuan (Figure 7.114).

***Sinicola biforis* (Heude 1885)**

Figures 7.17, 7.50

- 1885 *Helix biforis* Heude, 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, 111, pl. 30, Fig. 2 ["Ta-kouan tschen"].
- 1886 *Plectopylis biforis*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 188.
- 1887 *Helix biforis*, — Tryon, Manual of Conchology, 2 (3): 166, pl. 36, Figs 12–16 [China].
- 1896c *Plectopylis biforis*, — Gude, Science Gossip, 3: 156.
- 1897i *Plectopylis biforis*, — Gude, Science Gossip, 4: 103, Figs 57a–f.
- 1899e *Plectopylis (Sinicola) biforis*, — Gude, Science Gossip, 6: 148.
- 1899f *Plectopylis (Sinicola) biforis*, — Gude, Science Gossip, 6: 176.
- 2013 *Sinicola biforis*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 36, Figs 2 (map), 71, 80.

Types examined: Ta-kovan-tchen, Yun-nan, China. ex coll. Musée Heude, Shanghai, China acc. 1253, MCZ 167233/4 syntypes.

Diagnosis: A small, conspicuously angulated species with elevated, prominent callus with a strong but short apertural fold connecting it. Parietal wall with a vertical lamella and two horizontal plicae anteriorly near both sutures; between these plicae are some denticles.

Description: Shell discoid, almost flat; apex slightly raised; greyish-light brown; there are 6.25–6.75 slowly increasing whorls separated by a shallow suture; teleoconch irregularly, finely ribbed; ribs decussated with spiral lines; this fine structure is also visible on the ventral side; umbilicus moderately wide but deep; body whorl slightly keeled from ventral view hence, the umbilicus has an infundibular shape; apertural lip conspicuously thickened and reflected; callus curved, slightly elevated, with a short but high apertural fold attached; at both ends of the callus canals can be seen at the junction with the lip.

One specimen was opened. Parietal wall with a curved, vertical lamella and two horizontal plicae above and below anteriorly; parallel with the sutures; between the plicae there are three small denticles aligned in a row; palatal wall with six plicae; first very short, runs parallel with the suture; last also short, but longer than the first and slightly oblique; second plica very long, about two times longer than the 3rd–5th plicae; the remaining plicae are very variable, oblique, Z-shaped or bifurcated. In one specimen a ridge joined them.

Measurements (in mm): D= 11.4–13.3, H= 4.9–5.9 (n=4).

Differential diagnosis: The species resembles *S. jugatoria* however, denticles are lacking between the two horizontal plicae on the parietal wall while the apertural fold is missing. *S. asamiana* is smaller, has a more elevated spire and possesses no apertural fold.

Distribution: This species is known only from the type locality. The exact location of "Ta-kouan tschen" (the type locality) is uncertain. Johnson (1973) mentioned "Takouan" from Yunnan province and "Takouantschen" (31°10'N, 117°04'E) from Anhui Province. On the label of the type material however, the name of the province (Yunnan) is also stated. Therefore Johnson's (1973) "Takouan" (27°47'N, 103°50'E) is indicated on Figure 7.108 as the type locality of *S. biforis*.

Remarks: The figure depicted by Heude (1885) (the same republished by Gude 1897c) possibly shows an abnormal parietal lamellation. The figured specimen had two vertical lamellae on the parietal apparatus. Rare, multiple vertical lamellae are developed in some specimens. A similar case was described in *G. giardi* by Gude (1908b).

***Sinicola emoriens* (Gredler 1881)**

Figures 7.20, 7.50, 7.85, 7.92, 7.104

- 1881 *Helix emoriens* Gredler, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 8: 15 [westlich über der Grenze von Yün-Tscheou].
- 1882 *Helix fimbriosa*, — Heude, 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, 34, pl. 15, Fig. 5 (partim). ["Kieou Kiang", "Houang-tcheou", "Hou-nan meridionali"].
- 1883 *Plectopylis emoriens*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 10: 381 [in provincia sinensi Hunan].

- 1886 *Plectopylis emoriens*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 189.
 1887 *Helix fimbriosa* var. *emoriens*, — Tryon, Manual of Conchology, 2 (3): 158, pl. 34, Figs 32–35.
 1897g *Plectopylis emoriens*, — Gude, Science Gossip, 4: 36, Figs 50a–d.
 1899e *Plectopylis (Sinicola) emoriens*, — Gude, Science Gossip, 6: 148.
 1899f *Plectopylis (Sinicola) emoriens*, — Gude, Science Gossip, 6: 176.
 1939 *Plectopylis emorians* (sic!), — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg, 112, pl. 11, Fig. 15.
 2008 *Plectopylis emoriens*, — Zhouxing & Deniu, Farmland Molluscs from Zhejiang Province..., p. 245, Figs 127 a–b, 128, p. 383.
 2013 *Sinicola emoriens*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 36, Figs 89 (map), 91, 102.
 2014a *Sinicola emoriens*, — Páll-Gergely & Asami, Genus 25(3): 544–546, Fig. 16.

Types examined: Hunan, 3/5/1884, NHMW 108109/2 syntypes; Hunan, Coll. Gredler, 01/1881, NHMW 108110/2 syntypes.

Museum material examined: China: Hunan, Slg. Kobelt, alte Schau-slg, ex Gredler, orig: Yen (1939), pl. 11, Fig. 15, SMF 9269/1+1; China: Hunan, Slg. Möllendorff, SMF 42709/11; China: Guang-hsi, Slg. Möllendorff, SMF 42710/3; China: Hunan, Slg. O. Boettger ex Hungerford, 1890, SMF 42708/3; China: Hunan, Slg. Jetschin ex Schmacker, 1928, SMF 118083/2; China: Hunan, Slg. S. H. Jaekel, SMF 207671/1; China: Prov. Hunan, Slg. C. R. Boettger, 1904/43, SMF 118084/4; China: Hunan, Coll. Gerstenbrandt, NHMW 8457/2; Hunan, ex coll. Möllendorff, NHMW 8442/4; China, Hunan, Ex Museum Frankfurt, NHMUK 1882.5.9.19–20/2; China, coll. Godwin-A. (ex. Hungerford), NHMUK 1903.7.1.805/2; Hunan, coll. Denis, MNHN/2; Chine, Hunan, Coll. Letellier, 1949, MNHN/1; Hunan MNHN/1; Hunan ex Gredler, ex Schneider 29.VI.90, RBINS/2; China, Hunan, ex coll. Mus. Berlin, NHMSB 131/12, 122202 (1 specimen); China, Hunan, ex coll. Gredler, 1889, NHMSK 4817/6; China, Hunan, ex coll. Eastlake, J. W., USNM 161708/1; China, Hunan, ex coll. Möllendorff, USNM 195829/4.

New material examined: 2010/41 Hunan, Yongzhou Shi, Lingling Qu, Dengjiachong, rocky wall, 125 m, 26°13.808'N, 111°35.907'E, leg. Hunyadi, A., 8.11.2010, SMF 341517/2, HA/239, PGB/6; Guangxi, Guilin Shi, Yangshuo Xian, Xingping Zhen N 5 km, 170 m, 24°57.358'N, 110°31.857'E, leg. Hunyadi, A., 15.10.2009, HA/7, PGB/2; Guangxi, Quanzhou Xian, Quanzhou Zhen, Longyandong, leg. Ohara, K., Okubo, K. & Otani, J. U., 14.5.2010, OK/2; Hunan, Shuangpai Xian, Wulipai Zhen, near Qinglongdong, 26°00.83'N, 111°39.02'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 13.5.2010, OK/8, PGB/2; Hunan, Xiangxi Tujiazu Miaozu Zizhizhou, Jishou Xiang, Aizhai Zhen, Dehang Fengjingqu, Yuquanxi Jingqu, entrance of the gorge, 320 m, 28°20.611'N, 109°34.547'E, leg. Hunyadi, A., 26.10.2010, HA/1; Hunan, Yongzhou Shi, Lingling Qu, Chaoyangyan Gongyuan, 112 m, 26°12.525'N, 111°36.528'E, leg. Hunyadi, A., 8.11.2010, HA/109; Guangxi, Guilin Shi, Guilin, northern slope of Diecaishan, leg. Hunyadi, A., 16.10.2009, HA/7, PGB/2; Hunan, Feng Chuiya (?), collector not recorded, JG/2; Guangxi, Yangshuo Xian, Yangshuo Zhen, Mushan, 126 m, 24°46.342'N, 110°31.301'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/17, PGB/2.

Diagnosis: A very small, brownish *Sinicola* species with prominent sculpture, thick apertural lip without a callus. Parietal wall with a lamella and two anteriorly located plicae, one above and one below.

Description: Shell discoid, almost flat; brownish; dorsal side of teleoconch with rough reticulated sculpture; every third-fifth rib remains on the lower half of the body whorl; deciduous folds present on the keel of the body whorl; umbilical side almost smooth with inconspicuous growth lines only; the 4.5–5 whorls are separated by a deep suture; umbilicus moderately wide but very deep; apertural lip conspicuously thickened and slightly reflected; callus missing, but sometimes a white calcareous deposition can be seen on the penultimate whorl.

Six specimens belonging to different populations were opened. Parietal wall with a single lamella and two anteriorly located horizontal plicae; one above and one below; palatal wall with six parallel, horizontal or slightly oblique plicae.

Differential diagnosis: *S. emoriens* is much smaller than other *Sinicola* taxa without a parietal callus (*S. fimbriosa*, *S. reserata azona*). *S. stenochila* has sharper keel and some denticles before the lamella on the parietal wall.

Measurements (in mm): D= 6.6–8.6, H= 3.2–4.1 (n=6, shells from different localities).

Characters of the genital structure: One specimen was dissected (locality: Hunan, Yongzhou Shi, Lingling Qu, Dengjiachong, rocky wall, 125 m).

The right ommatophoral retractor crosses the genitalia. Penis consists of a long slender proximal end and a very short thicker distal portion; distal end of the penis linked to the epiphallus by weak muscle fibres; inner penis wall with approx. 14, more or less equally and folds, which continue into the epiphallus; no hooks were found in the

penis lumen. Penis more than three times longer than the epiphallus; retractor muscle very slender, it attaches to the long penial caecum; the retractor muscle-penial caecum transition not easily visible; vas deferens very long. Base of the vagina without swelling; distal vaginal section with several short muscle fibres on one side. Gametolytic sac slender and relatively long; another organ with unknown homology is grouped together with the gametolytic sac.

Radula: Figure 7.104 and Table 7.4.

Distribution: Material from north-eastern Guangxi, Southern Hunan and from a single location in Northwestern Hunan has been collected. Heude (1882) reported this species from Houang-tcheou (Eastern Hubei) and Yen (1948) mentioned it from Lutzepu (Zhejiang Province). I did not view specimens from the last two locations. Therefore, locality data cannot be verified (Figure 7.113).

Remarks: The genital structure of the species was already described in a previous paper (Páll-Gergely & Hunyadi 2013). An additional specimen from the same locality was anatomically examined (collection data: 2010/41 Hunan, Yongzhou Shi, Lingling Qu, Dengjiachong, rocky wall, 125 m, 26°13.808'N, 111°35.907'E, leg. Hunyadi, A., 8.11.2010, specimens in coll. PGB). This specimen had 10 embryos developing inside the semitransparent capsule in the uterus. Calcareous granules were present in the capsule layers of only the three largest embryos, which were situated most closely to the genital opening. However, the other seven embryos had no granules. This may indicate that those embryos with granules belong to a single litter.

"*Sinicola emoriens* var. *nana*" (Möllendorff 1886)

1886 *Plectopylis emoriens* var. *nana* Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 187 ["In meridionali parte provinciae sinensis Hunan"].

1887 *Helix fimbriosa* var. *nana*, — Tryon, Manual of Conchology, 2 (3): 158.

1896d *Plectopylis fimbriosa* v. *nana*, — Gude, Science Gossip, 3: 180.

1899e *Plectopylis (Sinicola) fimbriosa* v. *nana*, — Gude, Science Gossip, 6: 148.

2013 *Sinicola biforis*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 38.

Diagnosis: According to the original description, the shell is much smaller (6 mm) than the nominotypical subspecies and the last whorl has a more acute peripheral angle.

Remarks: No type material was found in the Senckenberg Museum, where all Möllendorff's plectopylid types are housed. Without available material the identity of this subspecies (?) remains doubtful.

This taxon was originally placed under *Plectopylis emoriens*, but all authors used this name under *P. fimbriosa* without examining the type material.

***Sinicola fimbriosa* (Martens 1875)**

Figures 7.18, 7.31, 7.86, 7.105

1875a *Helix fimbriosa* Martens, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 2: 128, pl. 3, Fig. 6. [type locality not specified].

1881 *Helix fimbriosa*, — Gredler, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 8: 15, pl. 1, Figs 1.

1882 *Helix fimbriosa*, — Heude, 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, 34 (partim).

1883 *Plectopylis fimbriosa*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 10: 380, pl. 12, Fig. 11 ["ad monasterium Dshiu-fêng-sy in montibus Lüschan prope urbem Kiu-kiang (ipse), in provincia Hunan"].

1886 *Plectopylis fimbriosa*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 189.

1887 *Helix fimbriosa*, — Tryon, Manual of Conchology, 2 (3): 158, pl. 34, Figs 41–43 [Prov. Hunan, China].

1896d *Plectopylis fimbriosa*, — Gude, Science Gossip, 3: 179, Figs 24a–b ["Kioo-Kiang, Province of Kiang-Si" and "Hou-nan"].

1897g *Plectopylis fimbriosa*, — Gude, Science Gossip, 4: 37.

1899e *Plectopylis (Sinicola) fimbriosa*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Sinicola) fimbriosa*, — Gude, Science Gossip, 6: 176.

1939 *Plectopylis fimbriosa*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112, pl. 11, Fig. 10.

1960 *Plectopylis fimbriosa*, — Zilch, Handbuch der Palaeozoologie, 6 (2) Euthyneura, Fig. 2096.

1999 *Sinicola fimbriosa*, — Schileyko, Ruthenica, Supplement 2: 460, Fig. 539 ["Hainan, China"].

2013 *Sinicola fimbriosa*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 38, Figs 3–4, 89 (map), 90a–b, 94.

2014a *Sinicola fimbriosa*, — Páll-Gergely & Asami, Genus 25(3): 546, Fig. 4.

Types examined: China, Kiukiang, ZMB/MOLL 24865/2 syntypes.

Museum material examined: Luschan-Gebirge b. Kiukiang, Slg. O. Boettger ex B. Schmacker 1889, SMF 42716/3; China: Hunan (Affenberg), Slg. W. Kobelt ex Gredler, SMF 42712/1; China: Hunan, Slg. C. Boschex Tausch-Verein, SMF 172100/2; China, Prov. Hupei (Hupé), Slg. G. Naegele ex Gredler ex L. Fuchs, SMF 50070/2; China: Hunan, Slg. S. H. Jaekel, SMF 207672/1; China: Luschan-geb. bei Kiukiang, Slg. Jetschin ex B. Schmacker, SMF 118081/1; China: Prov. Hunan, Slg. C. Boettger, 1903/43, SMF 118082/3; China: Hunan, Slg. O. Möllendorff, SMF 42713/6; China: Hunan, Slg. Kobelt (alte Schau-Slg.) ex V. Gredler, SMF 42711/2; China: Hunan, Slg. O. Möllendorff, SMF 42715/9; China: Hunan, Slg. O. Möllendorff, SMF 42714/5; China: Hupei (Hupé), Slg. C. Boschex H. Rolle, SMF 172101/4; Hainan Coll. Gerstenbrandt, NHMW 3773/2; Hunan, 2/4/1884, NHMW/2; Hunan 01/1881, NHMW/2; Coll. Edlauer ex Gredler, NHMW 14748/2; Hunan, ex coll. Möllendorff, NHMW 8443/7; Lushan/Lushan, Carl BockEsq. NHMUK 1891.4.24, 177–8/2; Tonkin, H. E. J. Biggs. coll. 2258, NHMUK 20110348/2; Prov. Hunan, NHMUK 20110350/2; Hushan, China, Hushan collection ex Beddome, NHMUK 20110349/2; Hunan (China) ex Mus. Frankfurt, NHMUK 1887.5.9.9–10/2; Chine, Hunan, coll. Denis, MNHN/1; China, Coll. Letellier, 1949, MNHN/1; China, Luchan, Kiukiang, MNHN/2; Hunan, Coll. Jousseume, MNHN/1; China, Coll. Staadt, 1969, MNHN/1; Chine, coll. Putzeys, RBINS/1; Chusan, Kiukiang, China, Schmacker leg., RBINS/2; China, Hunan, NHMSB 137/74 128957 (1 specimen); Mittelchina, ex coll. Mus. Berlin, NHMSB 131/11, 122201 (1 specimen); China, Hunan, ex coll. Gredler, 1889, NHMSK 4818/3; China, Hunan, ex coll. Möllendorff, USNM 195830 (2 adult and 7 juvenile shells); China, Hupé, ex coll. Möllendorff, USNM 184905/2; China, Hupé, ex coll. Möllendorff, USNM 184904/1; Hunan, ex Gredler, SMNG 07805/1; Lushan, near Kingkiang, coll. Borcharding ex coll. Möllendorff, SMNG 12605/6; Lushan near Kiukiang, Altonaer Museum, coll. Schmacker, ZMH 45898/2; Hunan, ex museum Klagenfurt, ZMH 45897/1.

New material examined: 2010/3 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. Hunyadi, A., 20.10.2010, HA/5, PGB/2; Hunan, Zhangjiajie Shi, Tianmenshan Guojia Senlin Gongyuan, Yihongguan (rocks in the forest), leg. Hunyadi, A., 22.10.2010. HA/1; Hunan, Chenxi Xian, Houma Zhen, Yanzidong, 455 m, 27°51.284'N, 110°15.623'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.3.2009, OK/2; Hunan, Huaihua Shi, Luping Xiang, Lupingdongqun, farm road, 332 m, 27°40.774'N, 110°01.289'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 9.3.2009, OK/2; Hunan, Huaihua Shi, Huangyan Luyou Dujiaqu, Jinjidong, 876 m, 27°28.300'N, 110°04.109'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 9.3.2009, OK/2; Hunan, Ningxiang Xian, Huangcai Zhen, Qianfodong, 28°12.95'N, 112°08.03'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 11.5.2010, OK/1; **Deng2** Hunan, Huangcai town, Ningxiang Xian, Qianfodong (Thousand Buddha Cave), 350–380 m, 28°12' 53"N 112°08' 21"E, leg. Dengxin, PGB/5; Guangxi, Sanjiang Xiang, Limu Zhen, Yankou Cun, 210 m, 25°10.509'N, 110°56.366'E, leg. Ohara, K., Okubo, K. & Otani, J. U., OK/1.

Diagnosis: A middle-sized *Sinicola* species with a light band on the umbilical surface. Apertural lip thickened, callus absent, parietal wall with a lamella and two horizontal plicae above and below.

Description: Shell yellowish corneous or chocolate brown; lenticular; apex slightly elevated; the 6–6.75 regularly growing whorls are separated by a shallow suture; apex irregularly wrinkled; the last whorl of the protoconch rather regularly, very finely ribbed; teleoconch with rough reticulated sculpture; ribs dominate the inside walls of the umbilicus while the ventral surface (out of the umbilicus) of the shell is almost smooth, glossy; a light band encircles the outer rim of the umbilicus; aperture with white, thickened and conspicuously reflected lip; callus lacking.

Six specimens were opened from different populations. Parietal wall with a curved lamella and two plicae anteriorly without denticles in between; palatal wall with six parallel plicae, sometimes with an additional denticle above the posterior end of the last plica.

Differential diagnosis: *S. schmackeri* possesses a lighter, transparent, much thinner shell and thinner apertural lip. Additionally, in *S. schmackeri*, the lower horizontal plica is always in contact with the parietal lamella and is usually accompanied by additional plicae. *S. reserata reserata* is smaller, has a sharper keel and an elevated callus. *S. reserata azona* is smaller, has a relatively thinner apertural lip and the light band around the umbilicus is missing.

Measurements (in mm): D= 14.9–18.4, H= 7.1–8.1 (n=5, shells from different localities).

Characters of the genital structure: One subadult specimen was dissected (Hunan, Hengyang Shi, Nanyue Qu, Yuelin Xiang, southern part of Heng Shan, Chuanyan Shilin, near Ban Shanting, 590 m).

The right ommatophoral retractor crosses the genitalia. Penis consists of a slender proximal and a thicker distal portion, the transition is not conspicuous. Proximal section about two times longer than the distal section;

proximal part with weak muscle fibre; inner penis wall more or less equally ribbed; the ribs are visible on the distal section of the penis and continue into the epiphallus; no hooks have been found in the penis lumen; penis more than two times longer than the epiphallus, and about four times longer than the penial caecum. Measuring to penial caecum was not easy because it was bent to the distal part of the penis. Retractor muscle very slender and attached to the short penial caecum; vas deferens very long; base of the vagina without swelling, however, this characteristic is likely to develop in adulthood; middle section of the vagina with several muscle fibres on one side; no gametolytic sac was found, an aspect most likely due to minimal development of this organ.

Radula: Figure 7.105 and Table 7.4.

Distribution: According to the literature, this species lives in Hunan, Hubei and Guangxi. I have material only from Hunan Province. The locality data from Hainan (Schileyko 1999) is probably wrong. The literature mentions the species from Lushan (Province Jiangxi).

Remarks: Yan et al. (2007) made EST isozyme analysis of "*Plectopylis fimbriosa*". Their collection site (Guiyang Qianling Gongyuan, Guiyang Xiang Baoshan) is out of the known distributional range of *S. fimbriosa*. I had no possibility to see those specimens; therefore the locality data is questionable (Figure 7.113).

"*Sinicola fimbriosa* var. *hunanica*" (Schmacker & Boettger 1890)

1890 *Plectopylis fimbriosa* var. *hunanica* Schmacker & O. Boettger, Mitteilungen aus der Gebiete der Malakozoologie, 1–2: 4 ["Hunan"].

2013 "*Sinicola fimbriosa* var. *hunanica*", — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 40.

Diagnosis: According to the original description, the nominotypical form (*fimbriosa* from "Lüshan-Gebirge bei Kiukiang") has a larger, stronger shell, higher whorls and narrower umbilicus. The ratio of the width to height of the shell is greater in *hunanica*.

Remarks: The collection of Schmacker is housed at the Geological Department of the University of Bremen. However, unfortunately the type series could not be identified among the materials of Schmacker. Therefore, the identity of this subspecies (?) remains questionable.

***Sinicola jugatoria* (Ancey 1885)**

Figure 7.17, 7.105

1885 *Plectopylis jugatoria* Ancey, Bulletins de la Société Malacologique de France, 2: 127 ["Kouy Tschéou"] (July).

1885b *Plectopylis laminifera* Möllendorff, Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 11–12: 164 ["Badung provinciae sinensis Hubei"] (November–December).

1886 *Plectopylis jugatoria*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 190.

1886 *Plectopylis laminifera*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 183, 190, pl. 6, Fig. 1 [in regione Badung provinciae sinensis].

1887 *Helix laminifera*, — Tryon, Manual of Conchology, 2 (3): 165, pl. 36, Figs 23–24 [Prov. Hubai, China].

1889a *Helix laminifera* (sic!), — Heude, Journal de Conchyliologie, 37: 45.

1889b *Helix (Plectopylis) laminifera*, — Gredler, Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 21: 202.

1897a *Plectopylis laminifera*, — Gude, Science Gossip, 3: 204, Figs 30 a–c.

1899a *Plectopylis jugatoria*, — Gude, Science Gossip, 5: 240.

1899a *Plectopylis laminifera*, — Gude, Science Gossip, 5: 240.

1899e *Plectopylis (Sinicola) jugatoria*, — Gude, Science Gossip, 6: 148.

1899e *Plectopylis (Sinicola) laminifera*, — Gude, Science Gossip, 6: 148.

1899f *Plectopylis (Sinicola) jugatoria*, — Gude, Science Gossip, 6: 176.

1899f *Plectopylis (Sinicola) laminifera*, — Gude, Science Gossip, 6: 176.

1908a *Plectopylis jugatoria*, — Gude, Proceedings of the Malacological Society of London, 8: 89.

1908a *Plectopylis laminifera*, — Gude, Proceedings of the Malacological Society of London, 8: 89.

1939 *Plectopylis laminifera*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112, pl. 11, Fig. 18.

2008 *Plectopylis jugatoria*, — Wood & Gallichan, Biotir Reports: 3, pl. 13, Fig. 3.

2013 *Sinicola jugatoria*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 40, Figs 68–69, 93 (map).

Types examined: Kouy-Chéou, Melvill-Tomlin collection, ACNMW 1955.158.24237, syntype (holotype?) of *jugatoria*; China: Patung, Hupei, Slg. Möllendorff, SMF 9282 (lectotype of *Plectopylis laminifera*); China, Patung, Hubei, Slg. Möllendorff, SMF 9283 (6 paralectotypes of *P. laminifera*); China: Patung, Hupei, Slg. Möllendorff, SMF 9254 (1 paralectotype of *P. laminifera*); China, Badung, Hubei, Slg. Möllendorff SMF 9255 (7 paralectotypes of *P. laminifera*).

Museum material examined: China: Chang Yang, Slg. C. Boschex H. Rolle, SMF 172103/2; China: Hupei (Hupé), Slg. G. Naegele ex Gredler ex L. Fuchs, SMF 50069/2; China: Hupei, Slg. O. Reinhardt, SMF 42703/2; China: Hupei, Slg. Ehrmann ex Schluter, SMF 42705/1; China: Hupei, Slg. Kobelt (alte Schau-Slg.) ex V. Gredler, SMF 42702/1; Südl. China, slg. H. Kaltenbach(9383) – Köhler, SMF 294869/3; China: Hupei, Slg. C. Bosch, SMF 172104/4; China: Hupei, Slg. Jaeckel, SMF 207673/1; China, Badung, Hubei, Slg. Möllendorff, SMF 9284/3; China: Yen-ling, Sy-tschuan [Kwei-dshou], Slg. Möllendorff, SMF 42704/2; China, Badung, Hubei, Slg. C. Boettger, 1903, SMF 118094/2; Hupé (Gredler det.), NHMW 22884/4; West Hupé, ex coll. Gredler, NHMW 8850/6; China: Hupé, Coll. Rušnov ex coll. dr. Werner ex coll. W. Blume, NHMW/2; China, Coll. Edlauer ex Gredler, NHMW 14748/2; Hupé, China (opened), NHMUK 1916.3.16.19/1; Chang-Yang, China, Salisbury collection ex Beddome, NHMUK 20110351/2; Hubei 22/10/90 (Sow.), NHMUK 20110352/2; Hupé, China 17/5/94, NHMUK 20110353/2; Hupé, China Rolle C/R, NHMUK20110354/1; Changya, Carl BockEsq., NHMUK 91.4.24.32–5/4; Changyang, Col Denis ex coll. Möllendorff, MNHN/2+2; China, Hupé, leg.: Linter, Coll. Letellier 1949, MNHN/2; China, Hunan, Coll. Joussaeume, MNHN/1; China, Changyang, Coll. A. Ch. Boubée, MNHN/2; Pa Tong, ZMB/MOLL 40217/1; Changyang, ZMB/MOLL 98672/1; Hupé, China, ZMB/MOLL 75789/1; Changyang (China), Fulton 18.7.94.2/6 RBINS/2+2; Hupé (Chine), Schneider 17.5.96. RBINS/1; W. Hupé, China, Dr. Oberwimmer ex Gredler, RBINS/1; Chine, ex Fulton 23.XI. 93, 2/6 (1 specimen); China, Patong in Hupé, NHMSB 131/199, 122811 (1 specimen); Patong (world in bracket not readable on the original label), NHMSB 7/94, 4806–4810 (5 specimens); Patong in Hupé, ex coll. Gredler, 1889, NHMSK 4819/1; China, Hubei, ex coll. Rolle, USNM 198278/2; Hubei, Changyang, Altonaer Museum, ZMH 45899/1.

New material examined: Chongqing, Kai Xian, Hongyuan Xiang, near Longzuimiao, 340 m, 31°32.39178'N, 108°28.12452'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 6.5.2007, OK/10, PGB/2; **2010/25** Hubei, Yichang Shi, Changyang Tujiazu Zizhixian, Qingjiang Hualang Fengjingqu, Geheyan Shuiku, Wuluozhougli Shan, 260 m, 30°25.805'N, 110°59.254'E, leg. Hunyadi, A., 31.10.2010, SMF 341518/1, HA/20, PGB/4; Hubei, Yichang Shi, Changyang Tujiazu Zizhixian, Qingjiang Hualang Fengjingqu, Buddhist cave temple above Geheyan Shuiku, 2 km S of the dam, leg. Hunyadi, A., 31.10.2010, HA/1; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Badong Xian, Longping Xiang, Longping N 8 km, Gezihe Shilin (stone forest), 1230 m, 30°51.361'N, 110°09.173'E, leg. Hunyadi, A., 2.11.2010, HA/1; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Enshi Shi, Mufu Cun SW 3 km, Enshi Daxiagu, exit of the stonepath, 500 m, leg. Hunyadi, A., 5.11.2010, HA/2; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Enshi Shi, Taiyanghe Xiang, Suobuya Shilin Jingqu, Split Rock, 975 m, 30°34.663'N, 109°34.401'E, Hunyadi, A., 6.11.2010, HA/2; Hubei, Badong, under limestone, leg. Yang Hao, August 2008, JG/2.

Diagnosis: A small *Sinicola* species with an elevated parietal callus, no fold in the aperture and two horizontal plicae in front of the vertical lamella on the parietal wall; no denticles between the plicae.

Description: This description is based on material collected near Badong, the Type locality of *S. laminifera*. Shell chocolate brown; lenticular and dorsally convex; with a slight keel on the upper part of the body whorl; whorls, flat, 6–6.5 in number, separated by a shallow suture; teleoconch with coarse riblets and spiral structure; on the apical part the sculpture is stronger; the ventral side almost smooth; umbilicus moderately wide and very deep; aperture white; lip reflected and slightly thickened; callus elevated, conspicuous, almost straight.

Six specimens were opened belonging to different populations. The specimen figured by Gude (1897a, Fig. 30c) was also observed (NHMUK). Parietal wall with a curved vertical lamella and two plicae above and below on the anterior side; very rarely an additional horizontal plica present between the two common plicae (see Gude 1897a). Palatal wall with a small, short horizontal plica near the suture, and four stronger and longer, nearly horizontal plicae, descending a little posteriorly and a short horizontal fold near the lower suture.

Differential diagnosis: *S. jugatoria* is larger than *S. asamiana*, has a wider umbilicus while in front of the vertical lamella there are no small denticles. It has a more elevated spire than *S. reserata* and has no denticles between the horizontal plicae on the parietal wall (see also under *S. reserata*). *S. jugatoria* is sympatric with *S. reserata azona* by Suobuya Shilin Jingqu. *S. jugatoria* can easily be distinguished by the presence of the elevated callus.

Measurements (in mm): D= 12.6–14.7, H= 6.3–7.0 (n=4, shells from different localities).

Radula: Figure 7.105 and Table 7.4.

Distribution: I have material with exact location data from Northern Chongqing and Eastern Hubei. Most of the museum material examined are from Hubei, but there is a sample from Guizhou (SMF 42704) (Figure 7.114).

Remarks: The names *jugatoria* and *laminifera* were used simultaneously in the literature for a long time. Finally Gude (1908a) synonymised the two species after examining Ancey's type. This aspect was overlooked by Yen (1939, 1941), Jaeckel (1950) and Schileyko (2011). On the other hand, the type of *jugatoria* is somewhat flatter than the shells collected from Badong (Hubei Province; Type locality of *laminifera*). *S. jugatoria* was described from the Province of Guizhou which is very far from Badong, not even bordering with Hubei Province. Since only the holotype is known from Guizhou, the internal lamellae could not be observed. I maintain *laminifera* as the synonym of *jugatoria*, but insist that our present knowledge is not enough to solve the *jugatoria-laminifera* problem.

Jaeckel (1950) reported two juvenile flotsam specimens from Vietnam. This was cited by Schileyko (2011). I did not see these specimens, but the juveniles of *S. laminifera* cannot be distinguished from related species. Therefore this species probably does not live in Vietnam.

***Sinicola murata* (Heude 1885)**

Figures 7.20, 7.50, 7.87, 7.92, 7.105

1885 *Helix murata* Heude, 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, 111, pl. 30, Fig. 1 ["In ditione Tchen K'ou"].

1886 *Plectopylis murata*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 186.

1887 *Helix murata*, — Tryon, Manual of Conchology, 2 (3): 159, pl. 33, Figs 13–15 [Tchenkeou, China].

1898c *Plectopylis murata*, — Gude Science Gossip, 4: 284, Figs 72a–b.

1899e *Plectopylis (Sinicola) murata*, — Gude, Science Gossip, 6: 149.

1899f *Plectopylis (Sinicola) murata*, — Gude, Science Gossip, 6: 176.

1939 *Plectopylis murata*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112, pl. 11, Fig. 18.

2013 *Sinicola murata*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 43, Figs 81, 89 (map), 99.

2014a *Sinicola murata*, — Páll-Gergely & Asami, Genus 25(3): 546–547, Figs 17, 21E.

Type material: According to Johnson (1973), the location of the type is not known. The shells listed in the "New material examined" and one of Möllendorff's samples (SMF 42726) is identical with the original figures and description.

Museum material examined: Szechwan (Sy-tschuan), China, Slg. Möllendorff, SMF 42724/3+1 (ribbed ventral surface); China Szechwan, Yen-ling, Slg. Möllendorff, SMF 42726/3; China: Hupei (Hu-bei), Slg. Möllendorff, SMF 42725/7.

New material examined: Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghou Shan, Cuiyinghu to upper Jinli cable station, 1273 m, 30°56.27110'N, 103°28.75198'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 9.7.2007, OK/3, PGB/1; Sichuan, Qionglai Shi, Tiantaishan Zhen, Tiantaishan above Zhenzhupubu, 30°16.87597'N, 103°07.46883'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 12.7.2007, OK/5, PGB/2; **20070710B** Sichuan, Dujiangyan Shi, Qingchengshan Zhen, below Woyunsi, 1110 m, 30°54.33919'N, 103°33.40153'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 10.7.2007, PGB/2, OK/2; **20070708B** Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghou Shan, Sanlong Shuijingrongdong, 942 m, 30°55.15418'N, 103°29.72375'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 8.7.2007, OK/3, PGB/1; Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghoushan, Shenxiandong, 835 m, 30°54.61750'N, 103°30.97445'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 09.07.2007., JUO/2; Sichuan, Dujiangyan Shi, Taian Zhen, Qingchenghoushan, above lower station of Jinli cable station, 979 m, 30°55.62540'N, 103°29.08667'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 08.07.2007., JUO/1; Sichuan, Qionglai Shi, Tiantaishan Zhen, Tiantaishan Dengyuean, 1071 m, 30°16.78396'N, 103°07.22660'E, leg. Nakahara, Y., Ohara, K., Okubo, K. & Otani, J. U., 12.07.2007., JUO/2; Sichuan, Dujiangyan Shi, Qingchengshan Zhen, Jinbianyan, 860 m, 30°53.762'N, 103°33.101'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 16.09.2013.

Diagnosis: A very small, yellowish species with grid-like dorsal sculpture and smooth base. Parietal wall with a lamella and some small denticles anteriorly.

Description: Shell yellowish or light brown; lenticular, conspicuously angulated; strong deciduous folds on the keel; 5.75–6.25 whorls separated by shallow umbilical side (downwards from the keel) with only low growth lines, the surface is shiny; umbilicus relatively narrow, but very deep; aperture with a relatively thin margin, which is slightly reflected; callus missing, only white coloration is visible on the penultimate whorl.

Three specimens were opened. Parietal wall with a curved lamella and two horizontal plicae on the anterior side, parallel with the sutures; between the plicae 3–4 denticles aligned in a row; palatal side with six short, straight, horizontal or slightly oblique palatal plicae; they become slimmer posteriorly; the plicae are sometimes connected with a continuous ridge.

Differential diagnosis: *S. murata* is larger and lighter than both subspecies of *S. stenochila*. Additionally, it has a relatively larger aperture, sharper keel and narrower umbilicus. *S. stenochila stenochila* is finely ribbed on the ventral surface, whereas *S. murata* is smooth. See also under remarks.

Measurements (in mm): D= 7.9–9.1, H= 3.8–4.9 (n=6, shells from different localities).

Characters of the genital structure: Two specimens were anatomically examined from two different localities: Sichuan, Dujiangyan Shi, Qingchengshan Zhen, Jinbianyan, 860 m, 30°53.762'N, 103°33.101'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 16.09.2013.; **20130917A** Sichuan, Dujiangyan Shi, Taian Zhen, Sanlongshuijing-rongdong, 1090 m, 30°55.039'N, 103°29.662'E, leg. Hosoda, T., Ohara, K., Okubo, K., Otani, J. U., 17.09.2013. Ethanol-preserved bodies are deposited in coll. PGB, respective shells in coll. JUO.

The right ommatophoral retractor crosses the male and female genitalia. Penis very long, rather spindle-shaped; inner wall of the distal portion is with 10–12 parallel folds; two of these folds become thickened proximally and connect at their proximal ends; penial caecum very short, pointed; epiphallus slender, cylindrical, about half as long as the penis; retractor muscle about twice as long as the penis, very slender. Vagina flat, slightly longer than the penis; equally wide to its proximal part, its distal end a bit more slender; proximal part of the vagina attached to the diaphragm with few slender fibres; vas deferens long, slender, and very slightly thickened at the end; gametolytic sac and the additional organ next to it are extremely long and very slender; only the gametolytic sac is slightly thickened. The uterus of the figured specimen from Jinbianyan contained six embryos, and the one from Sanlongshuijingrongdong had two embryos.

Radula: Figure 7.105 and Table 7.4.

Distribution: The species was described from Chengkou and is known from Hubei. I have material from Middle Sichuan. Sometimes it lives together with *Sic. invius* (Figure 7.113).

Remarks: Yen (1939) provided a description of the species and published one figure of a single specimen (SMF 42724). That specimen however, is not shiny on the ventral side (see the original description), and has a less sharpened keel. It may belong to a different (sub)species (probably related to *S. reserata azona*). However, without exact locality data and insufficient material its designation remains tenuous.

Sinicola murata differs from *S. stenochila* only in shell size, relative size of the aperture, and shell colour (Páll-Gergely & Hunyadi 2013). Anatomical features of *S. murata*, however, are more similar to those of *S. asamiana*, which also inhabits Sichuan. Both species have the extremely long penial retractor muscle, short penial caecum and several long, widely-spaced muscle fibres along the vagina. *S. stenochila* differs from these species by having the extremely long and terminally pigmented penial caecum of which the short and divided retractor muscle is attached, and the vaginal muscle fibres which are restricted to the vaginal bulb.

Sinicola reserata (Heude 1885)

Diagnosis: A small, variable species with slightly elevated spire, somewhat thickened, weak or missing callus. Parietal wall with a lamella and two horizontal plicae located anteriorly; between the plicae sometimes (3–4) denticles aligned in a row. In case of *S. reserata hensanensis* four plicae anteriorly located almost equidistant from each other.

Differential diagnosis: *Sinicola jugatoria* is darker, has a slightly narrower umbilicus and a less prominent keel than in *S. reserata*. *Sinicola asamiana* is smaller, has less sharp keel and a narrower umbilicus. *Sinicola biforis* has a well-developed callus and an apertural fold. *Sinicola fimbriosa* is larger and has a light band around the umbilicus.

General distribution: The species is known from Chongqing, Guizhou, Hunan and Hubei Provinces.

Sinicola reserata reserata (Heude 1885)

Figure 7.18

1885 *Helix reserata* Heude, 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, 111, pl. 30, Fig. 3 ["In ditione Tchen K'eu"].

1886 *Plectopylis reserata*, — Möllendorff, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 13: 190.

1887 *Helix reserata*, — Tryon, Manual of Conchology, 2 (3): 166, pl. 36, Figs 38–41 [Tchenkeou, China].

- 1889a *Helix reserata*, — Heude, Journal de Conchyliologie, 37: 45.
 1889b *Helix (Plectopylis) reserata*, — Gredler, Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 21: 202.
 1897g *Plectopylis reserata*, — Gude, Science Gossip, 4: 37, Figs 51a–e.
 1899e *Plectopylis (Sinicola) reserata*, — Gude, Science Gossip, 6: 148.
 1899f *Plectopylis (Sinicola) reserata*, — Gude, Science Gossip, 6: 176.
 1939 *Plectopylis reserata*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112, pl. 11, Fig. 11.
 2013 *Sinicola jugatoria*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 45, Figs 2 (map), 42.

Types examined: Tchen-K'ou, China, ex coll. Musée Heude, Shanghai, China (Acc.1253), lectotype MCZ 167130, paralectotypes MCZ 374359/17; Tchen-K'ou, coll. Chamberlain, USNM 472160 paralectotype.

The type lot received from Cambridge was a mixed sample. It contained 18 shells of *reserata* and one shell of *S. asamiana*. Therefore, a lectotype of *S. reserata reserata* is designated.

Museum material examined: China: Kweidshou, Yen-ling, (Sy-tshuan), SMF 42717/1+1.

Diagnosis: A small, strongly angulated and flattened *Sinicola* subspecies with elevated callus. Parietal wall with a lamella and two horizontal plicae located anteriorly; between the plicae some (3–4) denticles aligned in a row.

Description: Shell yellowish corneous; depressed conical, conspicuously angulated; teleoconch with spiral and ribbed structure of the same strength; the sculpture is also visible on the ventral surface; aperture relatively small; apertural rim slightly thickened and reflected; most of the specimens have an elevated callus, which is thinner than the apertural lip and is joined by two canals.

Two specimens were opened. Parietal wall with a vertical lamella with two horizontal plicae with 3–4 denticles in between; palatal wall with six parallel, short plicae.

Differential diagnosis: *S. reserata azona* is slightly smaller and has only a weak callus. Some specimens possessing the weak callus in the type lot of *S. reserata reserata* were indistinguishable from *S. reserata azona*. On the other hand, I retain *azona* as the subspecies of *reserata* instead of synonymizing it because the exact locality of *S. reserata reserata* is unknown and I have no newly collected material of *S. reserata reserata* to adequately address this problem.

Measurements (in mm): D= 11.4–13.3, H= 4.9–5.9 (n=4, MCZ 374359).

Characters of the genital structure: One specimen was dissected. Ethanol-preserved body is deposited in coll. PGB, respective shell in coll. JUO. Locality information: **20090308B** Guizhou, Tongren Shi, Wanshanchen dirt road, Xianrendong, 863 m, 27°31.785'N, 109°13.008'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.5.2010.

The right ommatophoral retractor crosses the male and female genitalia. Penis relatively long, spindle-shaped, slightly thickened at its middle part; internally with several longitudinal folds which form small "pockets" with the neighbouring ones, in the whole distal portion of the penis; penial caecum short, thickened; epiphallus slender, about half of the length of the penis; vas deferens slender, but becomes thicker near its insertion to the spermoviductus; retractor muscle slender and moderately long, it attaches to the end of the penial caecum. Vagina flat, with a slight "vaginal bulb"; vagina attaches to the diaphragm with a few rather long fibres; diverticulum and the gametolytic sac are long and slender, with the gametolytic sac slightly thickened. The anatomized specimen had a flat spermatophore with two round "packages", resembling two peas in a pod. A single, well-developed embryo was found in the uterus.

Distribution: This subspecies is known only from the type locality (Figure 7.108).

Sinicola reserata azona (Gredler 1887)

Figures 7.18, 7.88, 7.92, 7.96, 7.106

- 1887 *Plectopylis fimbriosa* var. *azona* Gredler, Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 14: 369 ["Westhupé auch an Sytschuan grenzt"].
 1889a *Plectopylis azona*, — Gredler, Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 21: 155.
 1896d *Plectopylis fimbriosa* var. *azona*, — Gude, Science Gossip, 3: 180.
 1897a *Plectopylis fimbriosa* var. *azona*, — Gude, Science Gossip, 3: 204.
 1899e *Plectopylis (Sinicola) azona*, — Gude, Science Gossip, 6: 148.
 1899f *Plectopylis (Sinicola) azona*, — Gude, Science Gossip, 6: 176.
 1939 *Plectopylis azona azona*, — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 113, pl. 11, Fig. 16.

2013 *Sinicola reserata azona*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 45, Figs 73, 93 (map).

2014a *Sinicola reserata azona*, — Páll-Gergely & Asami, Genus 25(3): 548–549, Figs 18, 20G, 21D, 21G.

Types examined: China: Hupei, orig. Yen (1939), pl. 11, Fig. 66, SMF 9260a, 1 syntype; China: Hupei, ex Gredler, SMF 9260/5 syntypes; Hupé, NHMW 31727/2 syntypes; Hupé, Chine, Schneider 29.11.91, RBINS/1 syntype.

Museum material examined: China, Prov. Hupei (Hubei) Slg. C. Boettger 1903/43, SMF 102816/5; China: Hupei, Slg. G. Naegle ex Gredler ex L. Fuch, SMF 50071/2; China: Hunan, Slg. O. Möllendorff, SMF 42707/4; Patong, Coll Edlauer ex Gredler, SMF 14745/2; Hupé, NHMUK 1900.2.13.222–223/2; Badung, Rock, July 04, NHMUK 20110355/2; Hupé, NHMUK 20110356/2; Hupé, China, Coll. Letellier ex Crosse, 1949, MNHN/1; Hunan, Coll. Jousseume, MNHN/1; Patong (world in brackets not readable on the original label), NHMSB 7/94, 4811 (1 specimen); NHMSB 7/95, 4812–4814 (world in brackets not readable on the original label) (3 specimens); China, Hupé, ex coll. Gredler 1889, NHMSK 4876/2; China, Badung, ex coll. Rolle, USNM 198271/1.

New material examined: Guizhou, Huangping Xian, Feiyun Ya (Feiyundong), 748 m, 26°57.130'N, 107°59.104'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 6.3.2009, OK/2, PGB/1; Hunan, Zhangjiajie Shi, Zhangjiajie Guojia Senlin Gongyuan, Tianzi Shan Jingqu, near Shuanghedong, 925 m, 29°22.931'N, 110°27.438'E, leg. Hunyadi, A., 24.10.2010, HA/4, PGB/4; Hunan, Chenxi Xian, Houma Zhen, Yanzidong, below the ranger station, 158 m, 27°52.053'N, 110°15.041'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.3.2009, OK/1; Hunan, Xiangxi Tujiazu Miaozu Zizhizhou, Yongshun Xian, Runya Xiang, Mayang Cun NW, rocks around the temple, west bank of the river in front of Maoyanhe Fengjingqu, 230 m, 29°09.123'N, 110°12.117'E, leg. Hunyadi, A., 23.10.2010, HA/15; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Enshi Shi, Taiyanghe Xiang, Suobuya Shilin Jingqu, Split Rock, 975 m, 30°34.663'N, 109°34.401'E, leg. Hunyadi, A., 6.11.2010., HA/3; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Enshi Shi, Taiyanghe Xiang, Suobuya Shilin Jingqu, Longgong, rocks in a coniferous forest, 915 m, 30°34.861'N, 109°34.544'E, leg. Hunyadi, A., 6.11.2010, HA/2; **2010/48** Hunan, Yongzhou Shi, Ningyuan Xian, Jiuyishan Yaozu Xiang N Jiuyishan Guojia Senlin Gongyuan, old maple (*Acer*) forest, 450 m, 25°21.200'N, 111°58.696'E, leg. Hunyadi, A., 11.11.2010, HA/1; Hunan, Sangzhi Xian, Lifuta Zhen, near Kuzhu He, 29°19.23'N, 110°08.15'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.5.2010, OK/3; **20090308B** Guizhou, Tongren Shi, Wanshanchen dirt road, Xianrendong, 863 m, 27°31.785'N, 109°13.008'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.5.2010, OK/2; Hunan, Dianfang town, Zhangjiajie City, 300 m, 28°58'N, 109°34'E, leg. Dengxin, PGB/2.

Diagnosis: A small, variable *Sinicola* taxon with thickened apertural lip and weak or missing callus. Parietal wall with a vertical lamella and two plicae anteriorly (one above and one below); between the plicae additional teeth are sometimes present.

Differential diagnosis: *Sinicola reserata azona* differs from typical *S. reserata reserata* specimens by the weaker (or missing) callus.

Characters of the genital structure: One specimen was dissected. Ethanol-preserved body is deposited in coll. PGB, respective shell in coll. JUO. Locality information: Guizhou, Tongren Shi, Wanshanchen dirt road, Xianrendong, 863 m, 27°31.785'N, 109°13.008'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.5.2010.

The right ommatophoral retractor crosses male and female genitalia. Penis relatively long, spindle-shaped, slightly thickened at its middle part; internally with several longitudinal folds which form small “pockets” with neighbouring ones, in the whole distal portion of penis; penial caecum short, thickened; epiphallus slender, about half the length of penis; vas deferens slender, but becomes thicker near its insertion to spermoviductus; retractor muscle slender and moderately long, attaching to the end of penial caecum. Vagina flat, with a weakly developed “vaginal bulb”; vagina attaches to diaphragm with a few rather long fibres; diverticulum and gametolytic sac are long and slender, with gametolytic sac slightly thickened. The anatomized specimen had a flat spermatophore with two round “packages”, resembling two peas in a pod. A single, well-developed embryo was found in the uterus.

Radula: Figure 7.106 and Table 7.4.

Measurements (in mm): D= 11.5–13.05, H= 5.2–6.4 (n=6, shells from different localities).

Distribution: *S. reserata azona* is known from Hunan, Guizhou and Hubei provinces (Figure 7.114).

Remarks: *S. reserata azona* was used as the subspecies of *S. fimbriosa* by several authors. However *azona* is closer related to *reserata* and its distribution overlaps with that of *S. fimbriosa*.

Sinicola reserata hensanensis (Yen 1939)

Figure 7.18

1939 *Plectopylis azona hensanensis* Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 113, pl. 11, Fig. 17 ["Heng-shan-hsien, Hunan"].

2013 *Sinicola jugatoria*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 46, Figs 2 (map), 74.

Types examined: Heng-shan-hsien, Hunan, coll. Möllendorff, holotype SMF 42814, paratype SMF 42815/1.

Diagnosis: A small *Sinicola* taxon with thickened apertural lip and very weak or missing callus. Parietal wall with a vertical lamella and four plicae anteriorly located almost equidistant from each other.

Differential diagnosis: *Sinicola reserata hensanensis* differs from *Sinicola reserata azona* by the four long plicae anterior to the lamella on the parietal wall. The Vietnamese *Gudeodiscus emigrans quadrilamellatus* (and seldomly *G. emigrans otanii*) has four long horizontal plicae on the parietal wall. These subspecies however are bigger and flatter with a wider umbilicus.

Measurements (in mm): D= 9.2, H= 4.4–4.8 (n=2).

Distribution: *S. reserata hensanensis* is known from the type locality only (Figure 7.108).

Sinicola schmackeri Páll-Gergely 2013

Figures 7.18, 7.49

2013 *Sinicola schmackeri*, — Páll-Gergely in Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 40, Figs 2 (map), 78a–c, 95.

1939 *Plectopylis lamifera* (!), — Yen, Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg: 112.

Type material: China: Sam-Kong-hue, Lien-dshou (Lianzhou?), Guang-dung, holotype SMF 341519, paratypes SMF 42706/7.

Diagnosis: A small, translucent, thin-walled *Sinicola* species with a thin apertural lip. On the parietal wall there is a lamella with 2–4 horizontal plicae anteriorly. The lowest plica is always attached to the vertical lamella.

Differential diagnosis: Due to the translucent shell wall, it was not necessary to open the body whorl. *Sinicola schmackeri* is smaller and lighter than *S. fimbriosa*, and the light band is missing from the umbilical side. The apertural rim is much slimmer and the lowest plica on the parietal wall is in contact with the lamella.

Measurements (in mm): D= 12.5–13.8, H= 5.2–6.1 (n=4).

Etymology: The type lot is housed in the Senckenberg Museum with Möllendorff's label bearing the name *schmackeri*. The type sample was probably collected by B. Schmacker.

Type locality: "Sam-Kong-hie, Lien-dshou, Guang-dshou."

Distribution: *Sinicola schmackeri* is known only from the type locality (Figure 7.108).

Remarks: I have found two localities under the name Lien-dshou (= Lianzhou). One is the suburb of Guangzhou (Miklós Szekeres pers. comm.), the other lies in Northern Guangdong (24°47'N, 112°23'E). The exact locality of the Type locality is therefore doubtful. Figure 7.108 shows the position of Lianzhou within Guangzhou. "Sam-Kong-hie" is likely an old name of a river (Miklós Szekeres pers. comm.).

Sinicola stenomphala Páll-Gergely & Hunyadi 2013

Figure 7.19

2013 *Sinicola stenomphala*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 47, Figs 93 (map), 96.

Type material: Guangxi, Guilin Shi, Longsheng Gezu Zizhixian, Longsheng Wenquan Guojia Senlin Gongyuan, hot spring SW 1300 m, 230 m, 25°54.197'N, 110°12.186'E, leg. Hunyadi, A., 13.10.2009, holotype HNHM 97453, HA/1.

Diagnosis: A small, conical *Sinicola* species with elevated spire and very narrow umbilicus. Parietal wall with a lamella with two horizontal plicae anteriorly, one above and one below.

Description: Shell light to dark brown; with conspicuously elevated spire appearing conical; teleoconch with rough, irregularly wrinkled sculpture of weak spiral striae; ventral side almost smooth; umbilicus very narrow and deep; aperture with very weak, only slightly thickened lip; elevated callus is missing, however indicated by a hint of white colouring on the parietal wall.

The holotype was opened. Parietal wall with a curved vertical lamella and two horizontal plicae anteriorly, one above and one below; palatal wall with five parallel plicae; the one most typically located near the upper suture is missing.

Differential diagnosis: This species differs from other species of the genus by its very narrow umbilicus and conspicuously elevated spire. There are only five plicae on the palatal wall, but the consistency of this character is unknown.

Measurements (in mm): D= 10.3–10.6, H= 5.6–5.8 (n=2).

Etymology: This species is named after its narrow umbilicus.

Type locality: Guangxi, Guilin Shi, Longsheng Gezu Zizhixian, Longsheng Wenquan Guojia Senlin Gongyuan, hot spring SW 1300 m, 230 m, 25°54.197'N, 110°12.186'E.

Distribution: *Sinicola stenophala* is known only from the type locality (Figure 7.114).

Sinicola stenochila (Möllendorff 1885)

Figures 7.19, 7.31, 7.34, 7.50, 7.89, 7.106

1885b *Plectopylis stenochila* Möllendorff, *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 11–12: 165 ["cum praec." = "Badung provinciae sinensis Hubei"].

1886 *Plectopylis stenochila*, — Möllendorff, *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 13: 186 [In regione Badung provinciae sinensis].

1887 *Plectopylis stenochila*, — Gredler, *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 14: 369.

1887 *Helix stenochila*, — Tryon, *Manual of Conchology*, 2 (3): 159, [Badung, Prov. Hubei, China].

1897a *Plectopylis stenochila*, — Gude, *Science Gossip*, 3: 204, Figs 29a–d.

1897g *Plectopylis stenochila* var. *basilia* Gude, *Science Gossip*, 38 (4): 36, Figs 49a–c ["Badung, Province Hoo-Pé, China"].

1899e *Plectopylis (Sinicola) stenochila*, — Gude, *Science Gossip*, 6: 148.

1899e *Plectopylis (Sinicola) stenochila* var. *basilia*, — Gude, *Science Gossip*, 6: 148.

1899f *Plectopylis (Sinicola) stenochila*, — Gude, *Science Gossip*, 6: 176.

1899f *Plectopylis (Sinicola) stenochila* var. *basilia*, — Gude, *Science Gossip*, 6: 176.

1900a *Plectopylis stenochila* var. *basilia*, — Gude, *The Journal of Malacology*, 7: 9, Fig. 6.

1939 *Plectopylis stenochila*, — Yen, *Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg*: 113, pl. 11, Fig. 22.

1939 *Plectopylis stenochila* var. *basilia* (as synonym of *stenochila stenochila*), — Yen, *Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg*: 113, pl. 11, Fig. 23.

2013 *Sinicola stenochila stenochila*, — Páll-Gergely & Hunyadi, *Archiv für Molluskenkunde* 142 (1): 47, Figs 89 (map), 98, 116–117.

2013 *Sinicola stenochila basilia*, — Páll-Gergely & Hunyadi, *Archiv für Molluskenkunde* 142 (1): 49, Figs 79, 89 (map), 93.

2014a *Sinicola stenochila*, — Páll-Gergely & Asami, *Genus* 25(3): 549–551, Fig. 19.

Types examined: China: Hupei, Patung (Badung), lectotype of *stenochila*, SMF 9267; China: Hupei, Patung (Badung), SMF 9268/12 paralectotypes of *stenochila*; Badung, Hupé, syntype of *stenochila* var. *basilia*, NHMUK 1922.8.29.97; China: Hubei, Badong, Slg. O. Boettger ex Möllendorff 1890, syntype of *stenochila* var. *basilia*, SMF 42731a/1; China: Hubei, Badong, Slg. O. Boettger ex Möllendorff 1890, syntype of *stenochila* var. *basilia*, SMF 42731b/1.

Museum material examined: China: Hubei, Badong, Slg. O. Boettger ex V. Gredler, 1887, SMF 42730/3; China: Hubei, Badong, Slg. C. Boschex H. Rolle, SMF 172107/2; China: Hubei, Badong, Slg. C. Boschex H. Rolle, SMF 172108/3; China: Hubei, Badong, Slg. Jetschin ex Oberwimmer 1907 ex SMF, SMF 118098/2; China: Hubei, Slg. W. Kobelt ex Möllendorff, SMF 42729/3; China (Gredler det.), NHMW 2285/3; Changyang (China), Coll. Gerstenbrandt, NHMW 7454/2; China: Hubei, Coll. H. Rolle, NHMW/2; China, Hubei, ex coll. Rolle, USNM 198290/2; C-China, ex Mus. Berlin, NHMUK 1890.12.27.12–13/2; Changya, China, Carl BeckEsq., NHMUK 91.4.24.21–4/4; Chang-Yang, NHMUK 1916.3.16.4/1; Chang-Yang 16/7/94, Jult C/R, NHMUK 20110357/2; Chang-Yang, China, Salisbury coll. ex Beddome, NHMUK 20110358/3; Chang-Yang, China, Coll. Denis, MNHN/1; Chang-Yang, China, Coll. Stadt 1969, MNHN/2; Changyang (China), Fulton 18.7.94.2/6, RBINS/2; China, Badung, ex coll. Rolle, USNM 198289/2; Badung, ex coll. Möllendorff, USNM 184692/3.

New material examined: 2010/30 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, SMF 341520/1, HA/33, PGB/6; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Badong Xian, Longping Xiang, Longping N 8 km, Gezihe Shilin (stone forest), 1230 m, 30°51.361'N, 110°09.173'E, leg. Hunyadi, A., 2.11.2010, HA/3; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Badong Xian, S of Chadianzi Zhen, Lianxia Fengjingqu, N of Liantoucao, 1025 m, 30°53.544'N, 110°18.995'E, leg. Hunyadi, A., 3.11.2010, HA/5; : Hubei, Badong Xian, Yanduhe Zhen, Shiyang Cun, 374 m, 31°11.98743'N, 110°21.46432'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.05.2007., OK/4; Chongqing, Chongqing Shi, Wushan Xian, Jianping Xiang, near toll station, 710 m, 31°03.05724'N, 109°55.51583'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 09.05.2007., OK/11 (one of them with smooth base); Chongqing, Chongqing Shi, Wushan Xian, Luoping Zhen, near toll station in Liziping, 1097 m, 31°11.55433'N, 110°04.46165'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 10.05.2007., OK/16 (one of them with smooth base); Chongqing Shi, Kai Xian, Hongyuan Xiang, near Longzuimiao, 340 m, 31°32.39178'N, 108°28.12452'E, leg. Ohara, K., Okubo, K. & Otani, J. U., 6.5.2007 (20070506E), OK/1, PGB/1; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Enshi Shi, Taiyanghe Xiang, Suobuya Shilin Jingqu, entrance of Liubuguan, in front of the Stone Sea Hotel, leg. Hunyadi, A., 6.11.2010, HA/1; Hubei, Enshi Tujiazu Miaozu Zizhizhou, Enshi Shi, Mufu Cun SW 3 km, Enshi Daxiagu, Mother-child Affection, 30°26.029'N, 109°10.260'E, leg. Hunyadi, A., 5.11.2010, HA/1; Guizhou, Sicheng Xian, Ganxi Xiang, Huayandong, leg. Ohara, K., Okubo, K. & Otani, J. U., 7.3.2009, OK/3, PGB/2.

Diagnosis: A very small species with smooth or finely ribbed ventral surface, moderately sharp keel and domed apical region. Parietal wall with one curved lamella and some denticles anteriorly.

Description: Shell lenticular, brown; consists of 5.75–6.25 regularly growing whorls; teleoconch sculpture of rather prominent and robust ribs; prominent spiral striae make for a reticulated dorsal surface; ventrally the ribs are dominant, while the overall sculpture is weaker; on the keel of the body whorl deciduous folds of the periostracum are detectable in fresh specimens; umbilicus moderately wide, but deep; body whorl rounded around the umbilicus; apertural lip thin, slightly reflected.

Six specimens were opened. Parietal wall with a vertical lamella and two parallel plicae anteriorly above and below; between these plicae usually two-three denticles are visible and sometimes joined; palatal wall with six relatively straight plicae; first and last slender and close to the sutures; the remaining plicae are supported by an additional denticle posteriorly; they are joined sometimes with the denticle.

Differential diagnosis: *S. murata* is slightly larger, lighter and has a relatively larger aperture. The similar *Sicradiscus cutisculptus* has weaker callus, and oblique palatal plicae, but it differs mainly in the parietal armature: it has a well-developed anterior lamella and a vestigial resorbed posterior one, of which only the two ends remain.

Measurements (in mm): D= 7.9, H= 3.9 (n=3, typical *stenochila* shells from different localities); D= 7.5–7.8, H= 3.9–4.1 (n=3, typical *basilia* shells from different localities).

Characters of the genital structure: Two specimens were anatomically examined. Collection information: **2010/30** 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. Ethanol-preserved specimens are deposited in coll. PGB.

The right ommatophoral retractor crosses the male and female genitalia. Penis very long, cylindrical, equally wide to the end; distal half of the penis internally with pockets which contained tiny calcareous granules; penial caecum very long, almost as long as the penis, but slightly more slender than the penis; distal end of penial caecum finely pigmented with transversal lines; two short, independent retractor muscles (or a single, basally divided one?) attaches to the distal end of the caecum; epiphallus shorter and slimmer than the caecum. Vagina about twice as long as the penis, with well-developed vaginal bulb in the middle; vagina attached to the diaphragm with several dense fibres on the vaginal bulb; vas deferens long, slender, but thickened at the end; gametolytic sac and the additional organ next to the gametolytic sac are moderately long, the gametolytic sac is more thickened than the additional organ.

Radula: Figure 7.106 and Table 7.4.

Distribution: This species is known from Western-Southwestern Hubei. I have material from the vicinity of Badong. However, several samples from old material were collected from Changyang, which lies about 100 km southeast of Badong. The exactitude of this locality is unknown. Su et al. (2007) reported this species from the Ziyang cave (Guizhou Province) but I was unable to observe these specimens. The locality in Guizhou is surprising in that it lies almost 400 km from the nearest known locality. I don't know whether it is an isolated population or if the distribution is continuous through Chongqing and Guizhou (Figure 7.113).

Remarks: Yen (1939) treated *Sinicola stenochila* var. *basilia* (Gude 1897) as a synonym of *Sinicola stenochila stenochila* (Möllendorff 1885) based on some *S. stenochila stenochila* specimens that bear as sharp keel as in *basilia*.

Páll-Gergely & Hunyadi (2013) distinguished these two forms based on the sculpture in the ventral shell surface (smooth in *basilia* and ribbed in *stenochila*), although specimens from Changyang showed intermediate shell characters between "typical" *stenochila* and *basilia*. New information revealed that smooth and ribbed specimens occur in the same new localities, which suggests that they represent variation within populations. Therefore, we conclude that *S. basilia* is a synonym of *S. stenochila* as proposed by Yen (1939). For anatomical notes, see under *S. murata*.

The *S. stenochila* shells displaying a smooth ventral surface are often labelled as "*glabrata*" (= bold) in the old collections. The name derives from Möllendorff, who recognized the difference between ribbed and smooth shells, but has not published the name.

***Sinicola straeleni* (Yen 1937)**

Figure 7.20

1937 *Plectopylis straeleni* Yen, Bulletin du Musée royal d'Historie Naturelle de Belgique, 13: 32–33, text Figs 4–6, pl. 2, Figs 1–1c ["Ning-hsiang, near Shun-kiang-kou, Hunan"].

2013 *Sinicola straeleni*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 49, Figs 2 (map), 100.

Types examined: Ning-hsiang, Hunan, RBINS 8B/9/f1, MT2325, 4 paratypes.

Description: According to Yen 1937: "Shell dextral, opaque but not thick, with a very low conical spire which being nearly depressed. Whorls 3 and 1/3, gradually increasing in width, and embracing to the ambital region. The apex is obtuse and prominent which being followed by 1 and 1/2 whorls bearing very fine, sparse but distinct lines of growth which are differentiated though not clearly marked off from its subsequent whorls by having considerably prominent sculptures present on the latter surfaces. Beginning from the final half of third whorl, the spiral lines appear decussating with the prominent growth lines. These sculptures are continuously present till the last whorl where they are traceable only above the angular periphery with but fine growth striae on the basal surface. The aperture is somewhat oblique, sublimate in outline, with its outer lip well thickened and slightly reflected, and inner lip thin but well defined. In breaking half volution of the body whorl, there is a series of five transversal plicae appearing on the outer wail, and one strong vertical lamina which being terminated with a less prominent horizontal one at each extremity on the parietal wail. The umbilicus is widely perspective and in moderate depth, with its external edge being obtusely angulated." The parietal armature has *fimbriosa*-type lamellation.

Measurements (in mm): D= 7.3–7.5, H= 3.8–3.9 (n=2, according to Yen 1937).

Distribution: The species is known only from the type locality (Figure 7.108).

Remarks: According to the original description, the holotype is in the private collection of the author (Yen). I could not find the location of Yen's collection. He died in Pennsylvania (Miklós Szekeres, pers. comm.) and his collection probably was in this state, too. The holotype could not be found in the collection of the ANSP (Paul Callomon, pers. comm.). The paratypes (all juvenile/damaged shells) from RBINS were examined. I cannot designate this species based on this material.

***Sinicola* (?) *vallata* (Heude 1889)**

1889a *Helix vallata* Heude, Journal de Conchyliologie, 37: 45 [Tchen K'ou].

1889b *Helix (Plectopylis) vallata*, — Gredler, Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 21: 202 [Tschen K'ou].

1899a *Plectopylis vallata*, — Gude, Science Gossip, 5: 240.

1899e *Plectopylis (Sinicola) vallata*, — Gude, Science Gossip, 6: 149.

1899f *Plectopylis (Sinicola) vallata*, — Gude, Science Gossip, 6: 176.

2013 *Sinicola vallata*, — Páll-Gergely & Hunyadi, Archiv für Molluskenkunde 142 (1): 49, Fig. 2 (map).

Description: Gude (1899a) translated and published Heude's description: "Shell discoid, lacinate at the periphery; below furnished with acute distant plaits, interspersed with minute striae trellis-like; lat. 10, alt. 5 millimetres. Tchen Keou. This *Plectopylis* recalls *P. stenochila*, but its dimensions are nearly double. Apart from the presence of the peripheral fringe, it may be stated that the inferior plaits are more numerous, and that their intervening spaces are trellised. These characters separate it from its congener of the right bank."

Remarks: According to Johnson (1973), no type material is available and most likely got lost. Figure 7.108 shows the type locality.

***Sinicola vargabalisti* Páll-Gergely 2014**

Figures 7.19, 7.33, 7.49.

2014a *Sinicola vargabalisti* Páll-Gergely in Páll-Gergely & Asami, Genus 25(3): 551–552, Figs 2–3, 5A–B, 22E–F.

Material: China, Guangxi, Laibin Shi, Wushan Xiang, ex coll. Yang Hao, 2013, HNHM 97455 (holotype), HNHM 97456 (paratype), PGB/3.

Diagnosis: A middle-sized, uniformly coloured *Sinicola* species with thickened apertural lip and a weaker callus. Parietal wall with a single lamella and two horizontal plicae anteriorly, one above and one below.

Description: Shell yellowish corneous or reddish brown; lenticular with domed apical part, the keel situated slightly above the middle line of the shell in apertural view; apex slightly elevated from the dorsal surface; the 6.25–7 (n=5) regularly growing whorls separated by shallow suture; finely and regularly ribbed protoconch consists of about two and a half whorls; dorsal side of teleoconch sculpture above the keel dominated by irregular radial ribs with some spiral lines between them; ventral side under the keel smooth; dorsal and ventral surfaces change discontinuously in morphology across the keel; keel with flat deciduous periostracal folds; these are sometimes visible on the preceding whorls on the dorsal surface of the shell; peristome whitish, thickened and reflexed, callus relatively weak but always present, slightly S-shaped and both ends of callus are separated by the peristome by shallow canals;

Two specimens were opened. On the parietal wall there is a curved lamella and two long horizontal plicae anteriorly without denticles in between; first palatal plica short and situated close to the suture; the last one also straight or curved downwards with an additional denticle above its posterior end; the remaining five plicae more or less horizontal and parallel, but usually depressed V-shaped with the longer arm of the "V" having anteriorly. One specimen had the "doubled" palatal plicae.

Differential diagnosis: In size the most similar species is *Sinicola fimbriosa*, which has the flatter shell with the shouldered body whorl. The keel of *S. vargabalisti* is lower in position in apertural view than *S. fimbriosa* and slightly above the middle line of the shell. Moreover, *S. fimbriosa* has a light band around the umbilicus, stronger reticulated surface on the dorsal side of the teleoconch, and six more regular and straight palatal plicae, whereas seven slightly V-shaped palatal plicae are present in *S. vargabalisti*. *S. fimbriosa* lacks the callus, but *S. vargabalisti* has the weak callus.

Measurements: (in mm, n=5): D= 16–19.5, H= 6.6–8.5.

Etymology: *S. vargabalisti* is named after my friend, Bálint Varga, to celebrate a 25 year-old friendship.

Distribution: The species is known only from the type locality.

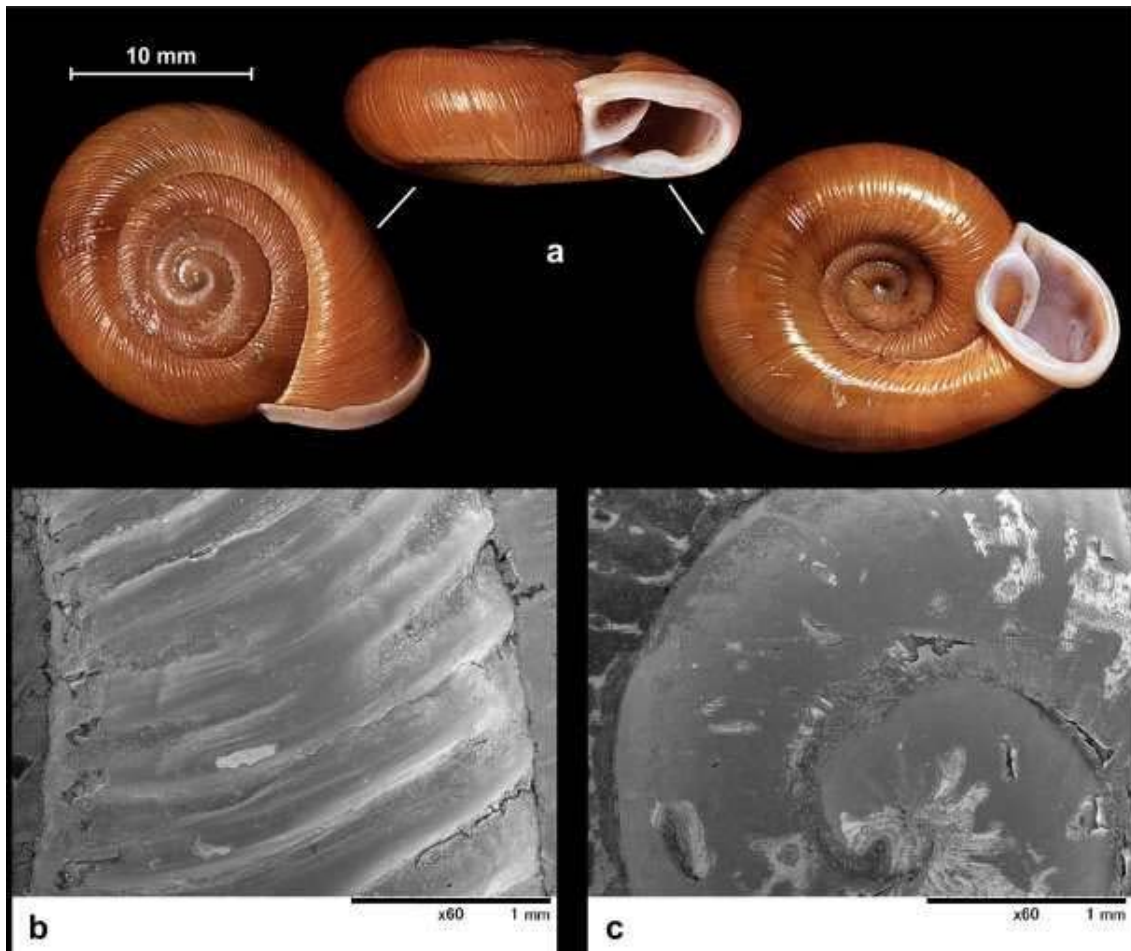


Figure 7.1. Shells and shell sculpture of *Corilla*. A: *Corilla erronea*, holotype, NHMUK, Photos: H. Taylor (NHMUK); B: penultimate whorl of *Corilla* sp., locality unknown, MHNH, coll Stadt, 1969; C: protoconch of *Corilla* sp., same data as Figure B.

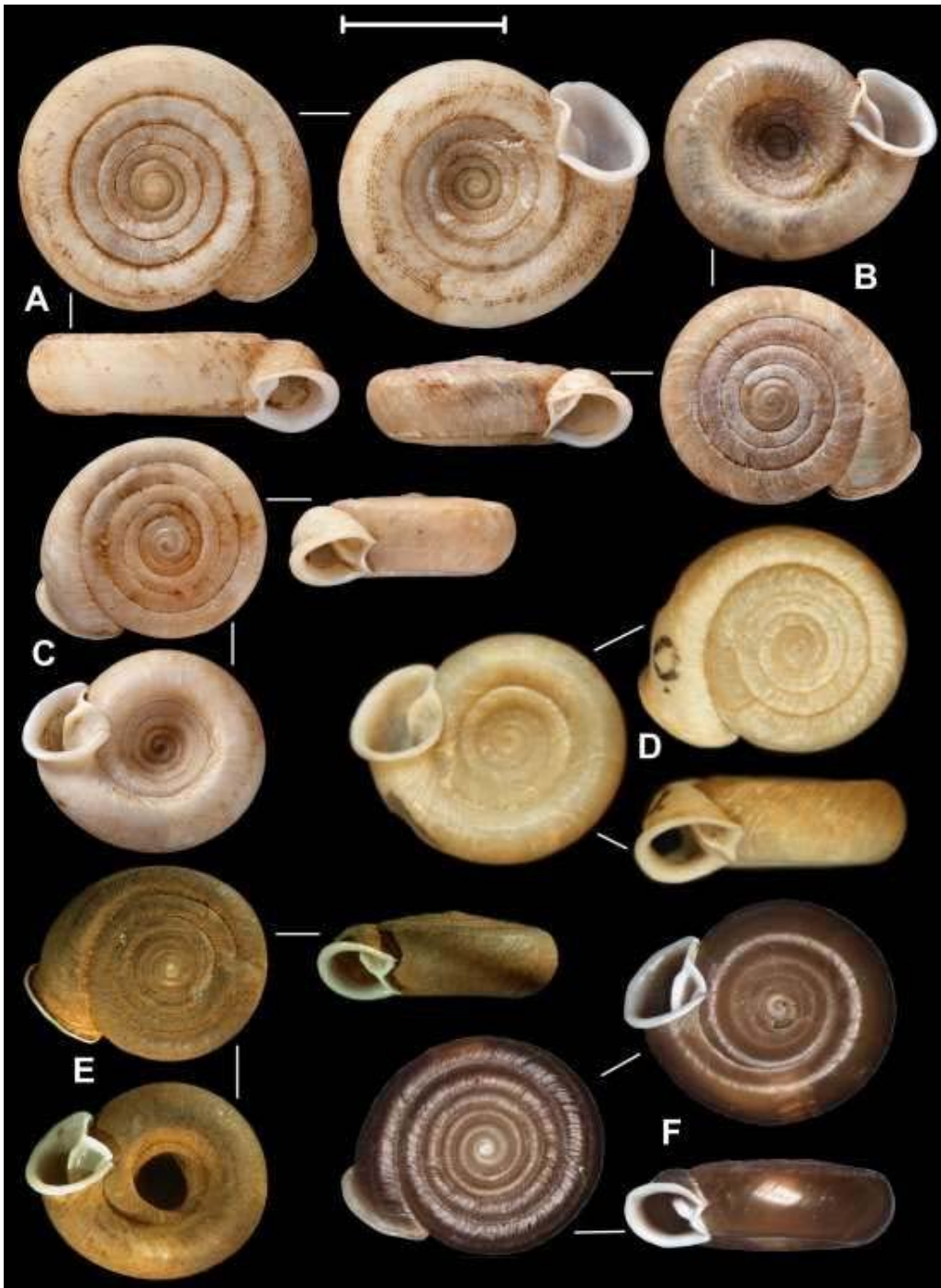


Figure 7.2. A: Genus1 (?) *austeni* (Gude, 1899), lectotype, 1903.06.01.1014., Photos: H. Taylor; B: Genus1 *dextrorsa* (Benson 1860), holotype, NHMUK 1906.2.2.144., Photos: H. Taylor; C: *Chersaecia refuga* (Gould 1846) (typical *leiophis*), NHMUK 1888.12.4.1526–1528., Photos: H. Taylor; D: *Ch. refuga*, lectotype, MCZ 169335, Photos: A. Baldinger; E: *Chersaecia goniobathmos* (Ehrmann, 1922), lectotype, SMF 150100a, Photos: B. Páll-Gergely; F: *Chersaecia shanensis* (Stoliczka 1873), 2009.10.18B, Photos: T. Deli. Scale represents 10 mm.

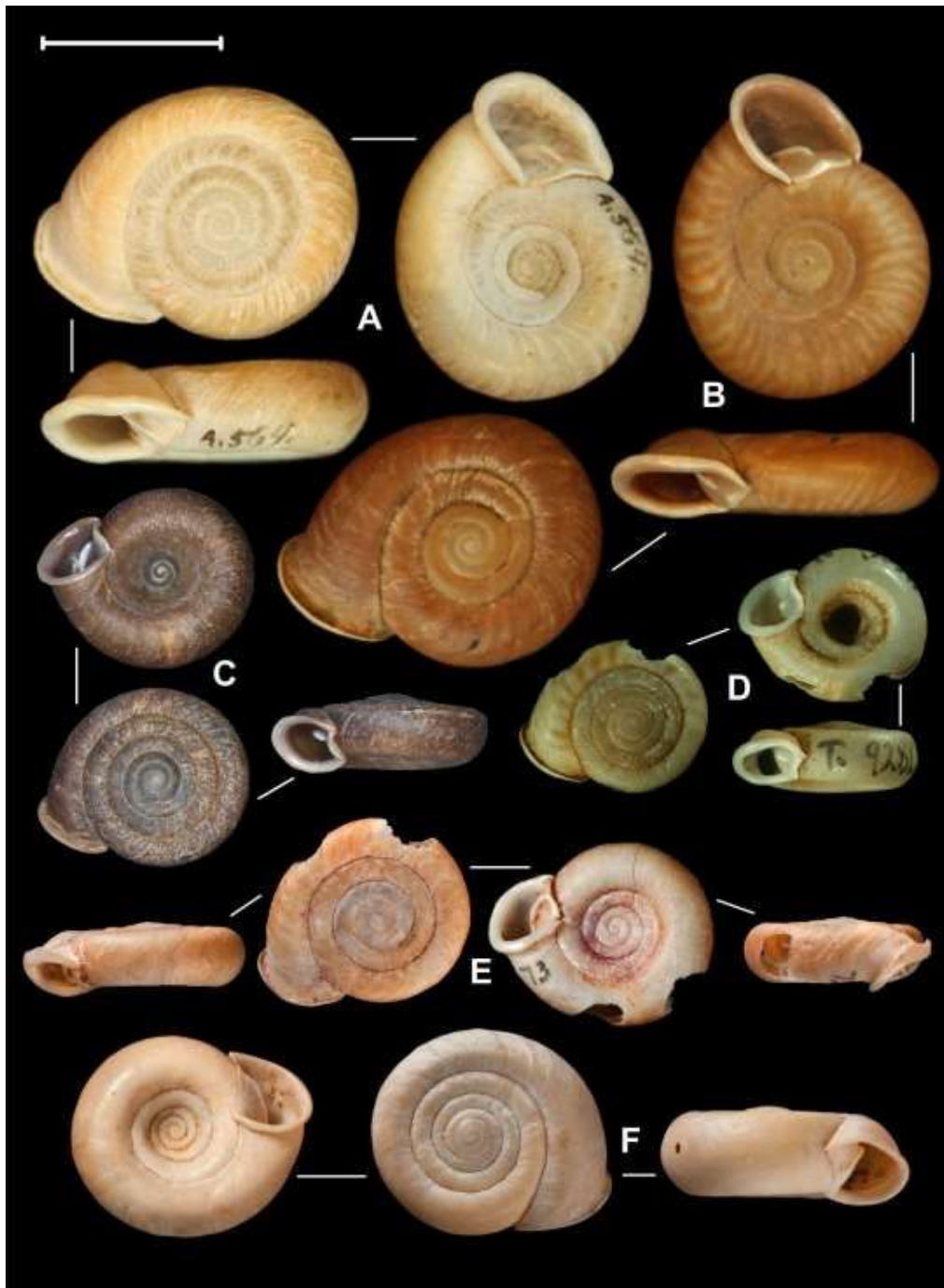


Figure 7.3. *Plectopylis bensoni* Gude 1914 (lectotype of *P. repercussa*, MCZ 169336), Photos: A. Baldinger; *Plectopylis anguina* (Gould, 1847), lectotype, MCZ 169042, Photos: A. Baldinger; *Plectopylis species2* u. sp. holotype, Photos: T. Deli; D: *Plectopylis linterae* Möllendorff, 1897, lectotype, SMF 9280, Photos: B. Páll-Gergely; E: *Plectopylis cairnsi* Gude, 1898, holotype NHMUK 1922.8.29.47, Photos: H. Taylor; F: *Endoplon brachyplecta* (Benson, 1863), paratype, NHMUK 1954.6.2.282., Photos: H. Taylor.



Figure 7.4. A: Genus3 *laomontana* (Pfeiffer, 1863), syntype, NHMUK 20130004, Photos: H. Taylor; B: Genus3 *laomontana*, 2006.10.13., Photos: T. Deli; C: Genus2 species3 u. sp., holotype, MNHN 24947, Photos: T. Deli; D: Genus2 *andersoni* (W. Blanford 1869), SMF 172066, Photos: E. Neubert; E: Genus2 *andersoni*, RBINS 10591, Photos: T. Deli. Scale represents 20 mm.

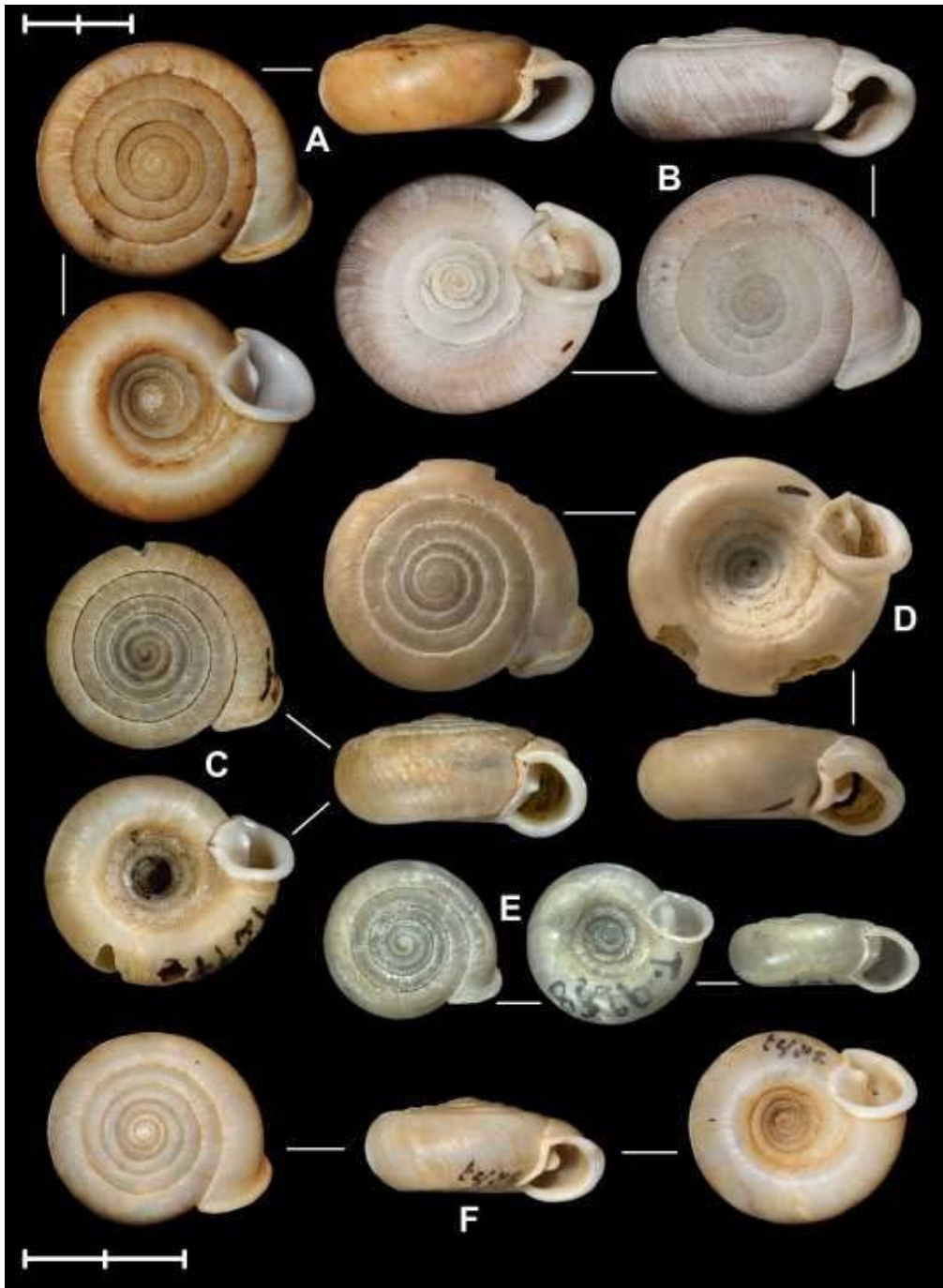


Figure 7.5. A: *Halongella schlumbergeri* (Morelet, 1886) syntype, MNHN 24582, Photos: T. Deli.; B: *Halongella schlumbergeri* (syntype of *jovia* Mabille 1887, MNHN 24580), Photos: T. Deli; C: *Halongella schlumbergeri* (lectotype of *hirsutus* Möllendorff 1901, SMF 9277), Photos: E. Neubert; D: *Halongella schlumbergeri* (holotype of *pilsbryana* Gude 1901, NHMUK 1922.8.29.52), Photos: H. Taylor; E: *Halongella fruhstorferi* (Möllendorff 1901), lectotype, SMF 9258, Photos: E. Neubert; F: *Gudeodiscus dautzenbergi* (Gude 1901), holotype, MNHN 24603, Photos: T. Deli. Scales represent 10 mm, small scale refers to *H. fruhstorferi* and *Plectopylis hirsuta* only.

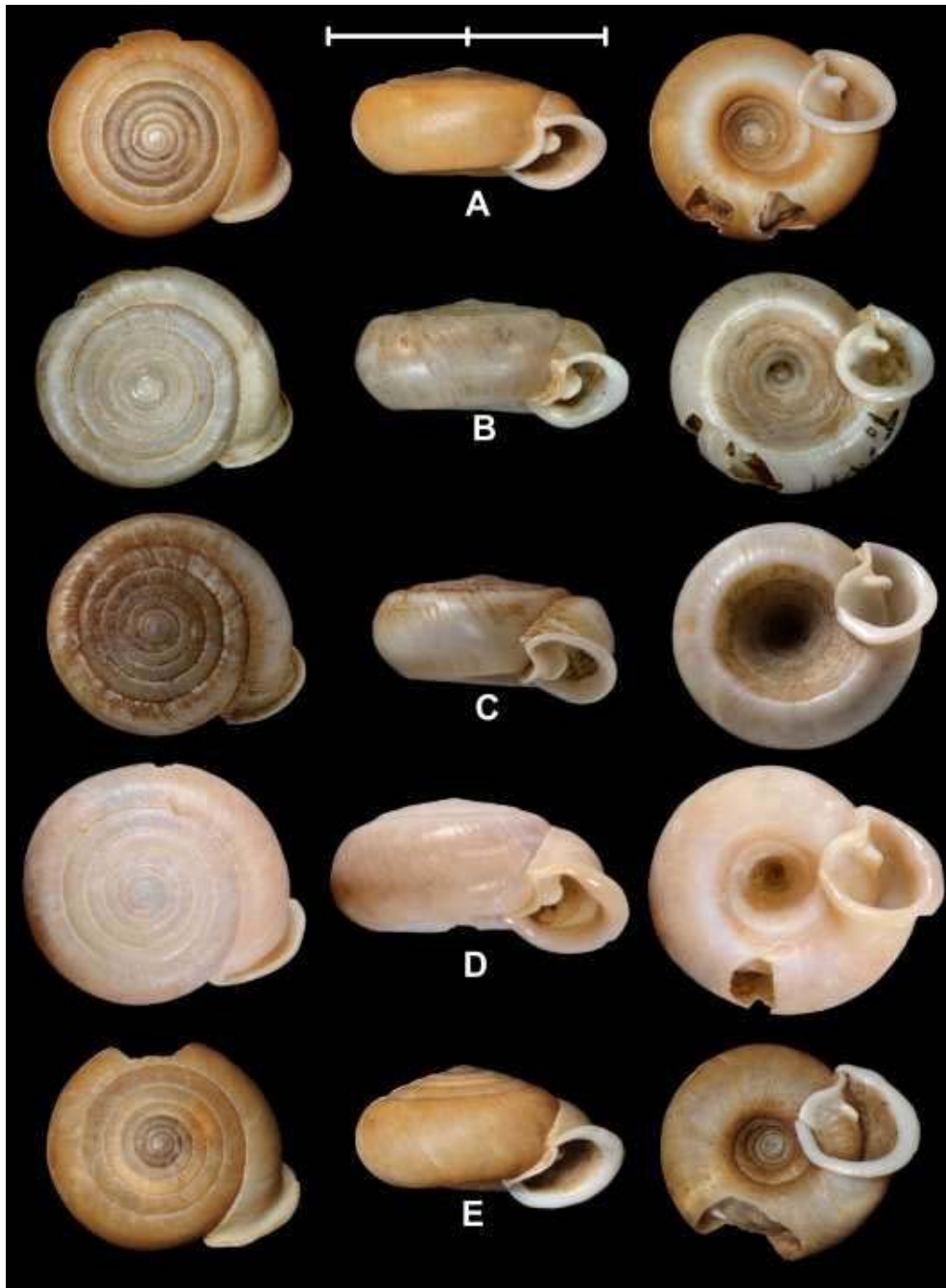


Figure 7.6. A: *Gudeodiscus dautzenbergi* (Gude 1901) (holotype of *persimilis* Gude 1901, MNHN 24602), Photos: T. Deli; B: *Gudeodiscus villedaryi* (Ancey, 1888), holotype, NHMUK 1930.9.12.38, Photos: H. Taylor; C: *Gudeodiscus villedaryi* (Ancey, 1888) (lectotype of *choanomphala*, SMF 9279), Photos: S. Hof; D: *Gudeodiscus villedaryi* (Ancey, 1888), Vn11-152, Photos: B. Páll-Gergely; E: *Gudeodiscus giardi* (H. Fischer 1898); MNHN 9946 (syntype of *giardi*), Photos: T. Deli. Scale represents 20 mm.



Figure 7.7. A: *Gudeodiscus giardi* (H. Fischer 1898), Deng1, Photos: T. Deli; B: *Gudeodiscus giardi* (H. Fischer 1898) (syntype of *Plectopylis congesta*, NHMUK 1922.8.29.49), Photos: H. Taylor; *Gudeodiscus giardi* (syntype of *Plectopylis congesta*, MNHN IM-2010-12120), Photos: T. Deli; D: *Gudeodiscus giardi szekeresi* Páll-Gergely & Hunyadi 2013, holotype HNHM 97450, Photos: T. Deli; *Gudeodiscus giardi oharai* Páll-Gergely 2013, holotype HNHM 97449, Photos: T. Deli. Scale represents 20 mm.

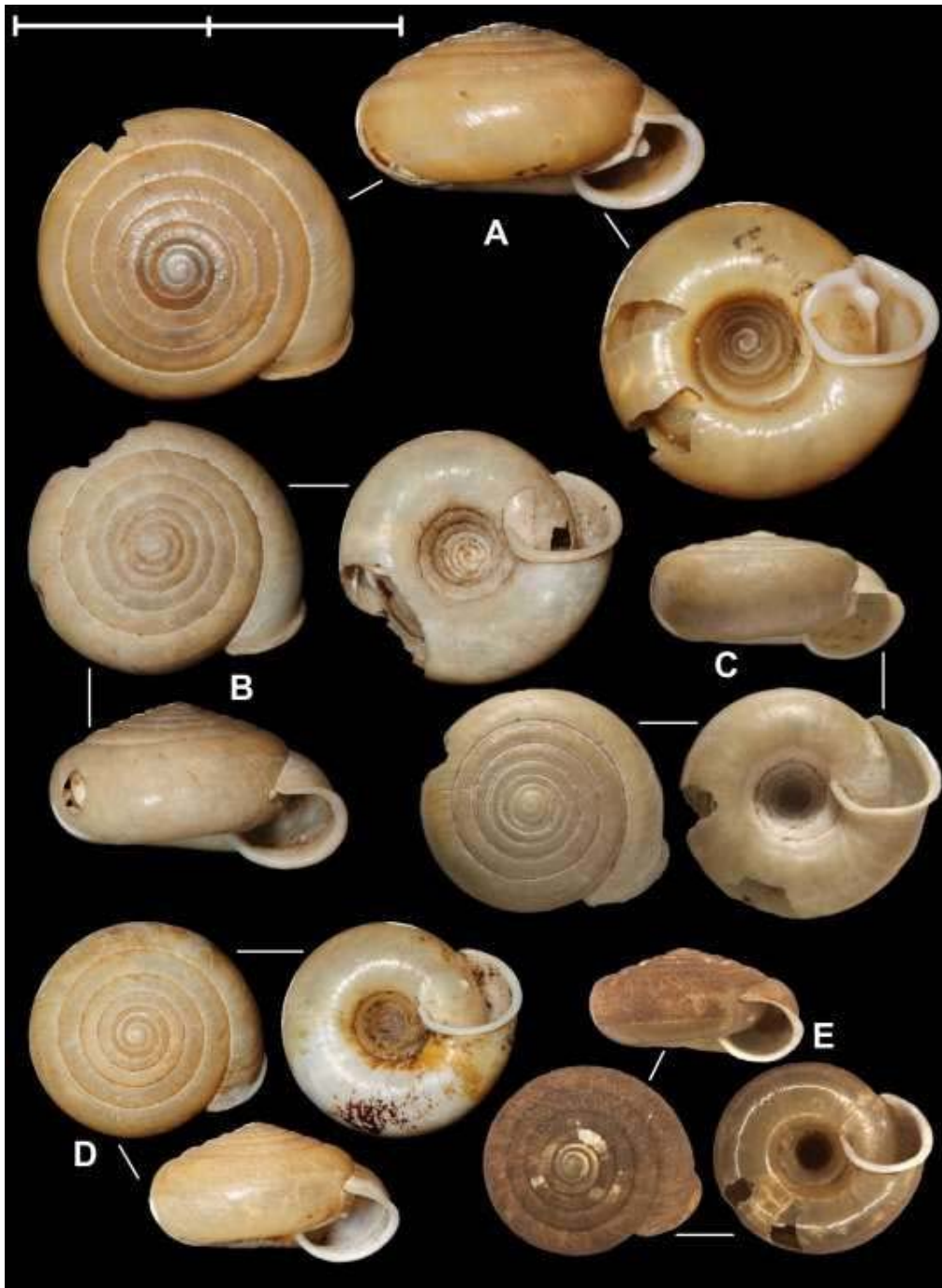


Figure 7.8. A: *Gudeodiscus (Gudeodiscus?) francoisi* (Fischer 1898), MNHN 24601 (holotype of *Plectopylis bavayi*), Photos: T. Deli; B: *G. (G.?) francoisi* (Fischer 1898), MNHN 9945 (holotype of *Plectopylis francoisi*), Photos: T. Deli; C: *G. (G.?) francoisi* (Fischer 1898), NHMUK 1922.8.29.51 (holotype of *Plectopylis lepida*), Photos: H. Taylor; D: *Gudeodiscus (Gudeodiscus?) suprafilaris* (Gude 1908), MNHN 24586 (holotype?), Photos: T. Deli; E: *G. (G.?) suprafilaris* (Gude 1908), 2011/81, Photos: B. Páll-Gergely. Scale represents 20 mm.



Figure 7.9. Shells of Vietnamese *Gudeodiscus* species. A: *Gudeodiscus (Gudeodiscus) fischeri* (Gude 1901), Vn10-120, Photos: B. Páll-Gergely; B: *G. (G.) fischeri* (Gude 1901), MNHN 24579 (holotype of *Plectopylis fischeri*); C: *G. (G.) fischeri* (Gude 1901), MNHN 24587 (holotype of *Plectopylis tenuis*); D: *G. (G.?) infralevis* (Gude 1908), MNHN 24604 (holotype of *Plectopylis infralevis*); E: *G. (G.?) infralevis* (Gude 1908), MNHN 24585 (holotype of *Plectopylis soror* Gude 1908). All Photos by T. Deli with the exception of Figure A. Scale represent 10 mm.



Figure 7.10. Shells of Vietnamese *Gudeodiscus* species. A: *Gudeodiscus multispira* (Möllendorff 1883) holotype, Photos: E. Neubert; B: *Gudeodiscus multispira* (Möllendorff 1883) 2009/90, Photos: T. Deli; C: *Gudeodiscus soosi* Páll-Gergely 2013, holotype, Photos: B. Páll-Gergely; D: *Gudeodiscus yunnanensis* Páll-Gergely 2013, holotype, Photos: J. Harl; E: *Gudeodiscus cyrtochilus* (Gude 1909), NHMUK 1922.8.29.59. (syntype), Photos: H. Taylor; F: *Gudeodiscus cyrtochilus* (Gude 1909), 2011/19. Scale represents 20 mm.

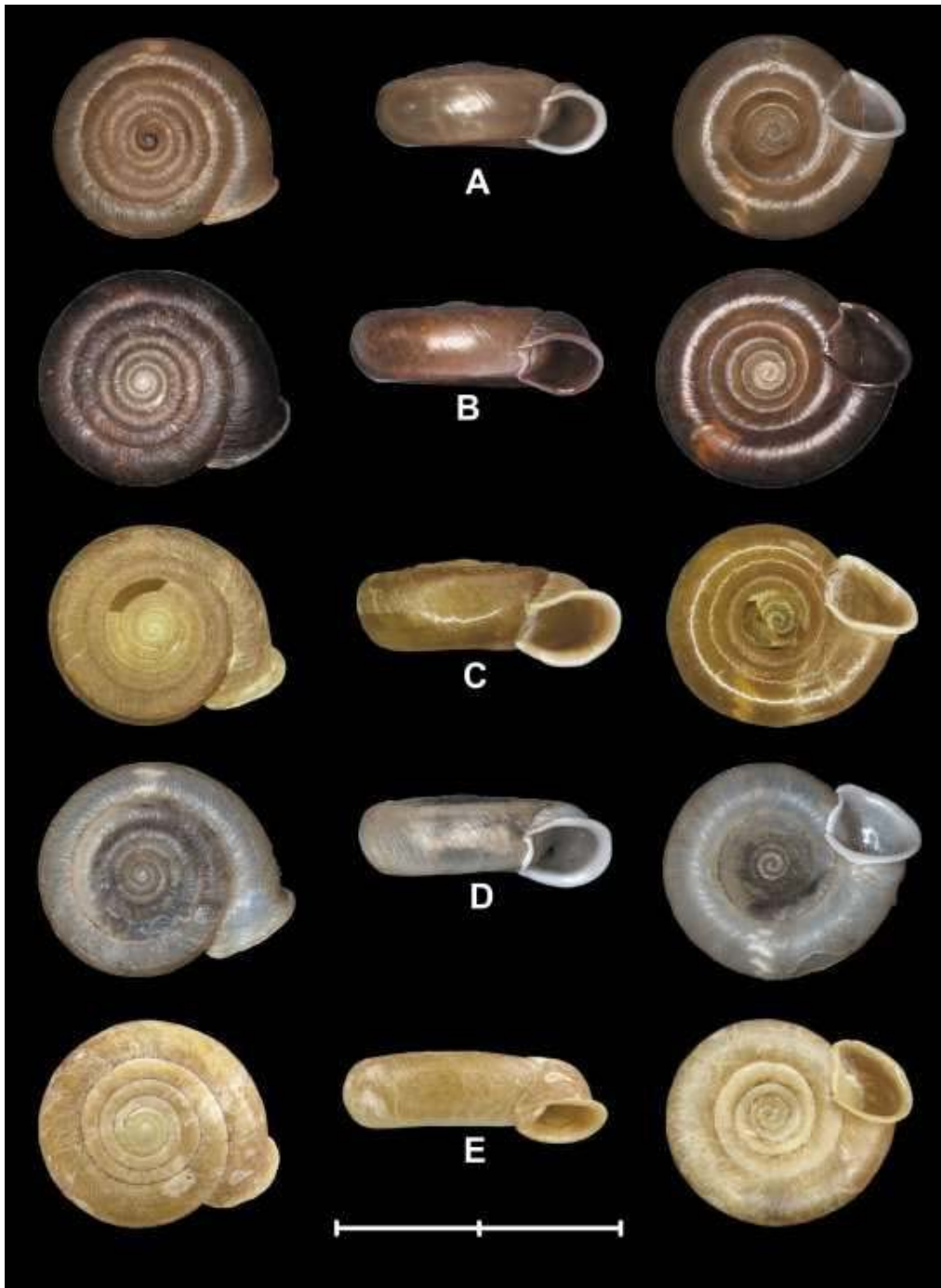


Figure 7.11. A: *Gudeodiscus eroessi eroessi* Páll-Gergely & Hunyadi 2013, Holotype, HNHM 97447, Photos: J. Harl & B. Páll-Gergely; B: *Gudeodiscus eroessi fuscus* Páll-Gergely & Hunyadi 2013, Holotype, HNHM 97448, Photos: J. Harl & B. Páll-Gergely; C: *Gudeodiscus eroessi hemisculptus* Páll-Gergely 2014, Holotype, HNHM 97484, Photos: B. Páll-Gergely; D: *Gudeodiscus okuboi* Páll-Gergely & Hunyadi 2013, Holotype, HNHM 97451, Photos: J. HARL & B. Páll-Gergely; E: *Gudeodiscus concavus* Páll-Gergely 2013, holotype, HNHM 97440, Photos: B. Páll-Gergely. Scale represents 20 mm.



Figure 7.12. A: *Gudeodiscus emigrans emigrans* (Möllendorff 1901), Lectotype, SMF 9256, Photos: E. Neubert; B: *Gudeodiscus emigrans otanii* Páll-Gergely 2013, Holotype, HNHM 97446, Photos: T. Deli; C: *Gudeodiscus emigrans otanii* Páll-Gergely 2013, Paratype, Photos: T. Deli; D: *Gudeodiscus emigrans quadrilamellatus* Páll-Gergely 2013, Holotype, HNHM 97468, Photos: J. Harl & B. Páll-Gergely. Scale represents 20 mm.

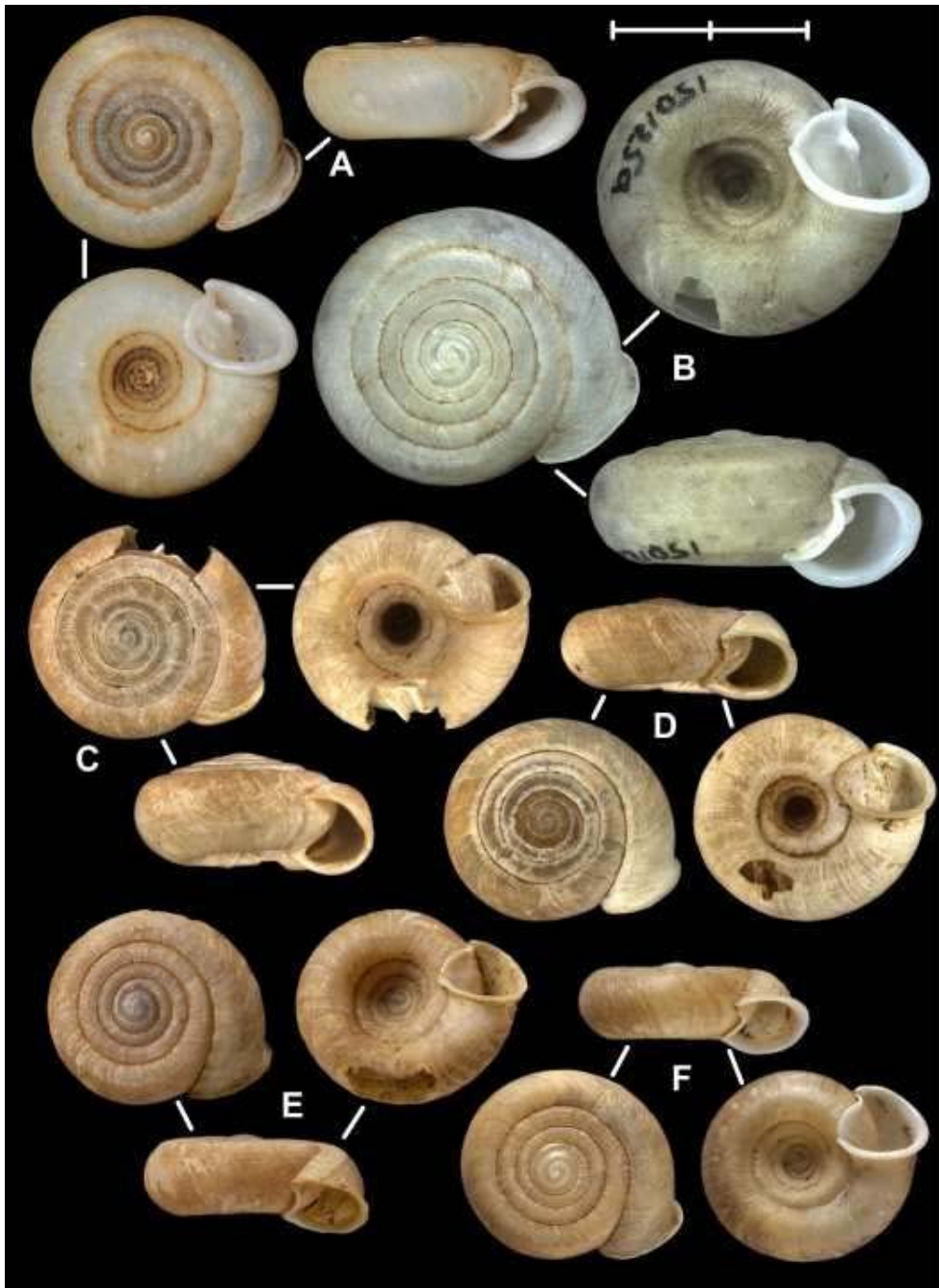


Figure 7.13. A: *Gudeodiscus phlyarius phlyarius* (Mabille 1887), MNHN 24581 (syntype of *Plectopylis phlyaria*), Photos: T. Deli; B: *Gudeodiscus phlyarius* (Mabille 1887), SMF 150125a (lectotype of *P. moellendorffi*), Photos: E. Neubert; C: *Gudeodiscus* cf. *phlyarius*, Vn10-41, Photos: B. Páll-Gergely; D: *Gudeodiscus phlyarius*, Vn09-06, Photos: B. Páll-Gergely; E: *Gudeodiscus phlyarius*, NHMUK 1922.8.29.56 (holotype of *P. gouldingi* Gude 1909), Photos: H. Taylor; F: *Gudeodiscus phlyarius*, NHMUK 1922.8.29.57. (holotype of *Plectopylis anterides* Gude 1909), Photos: H. Taylor. Scale represents 10 mm.

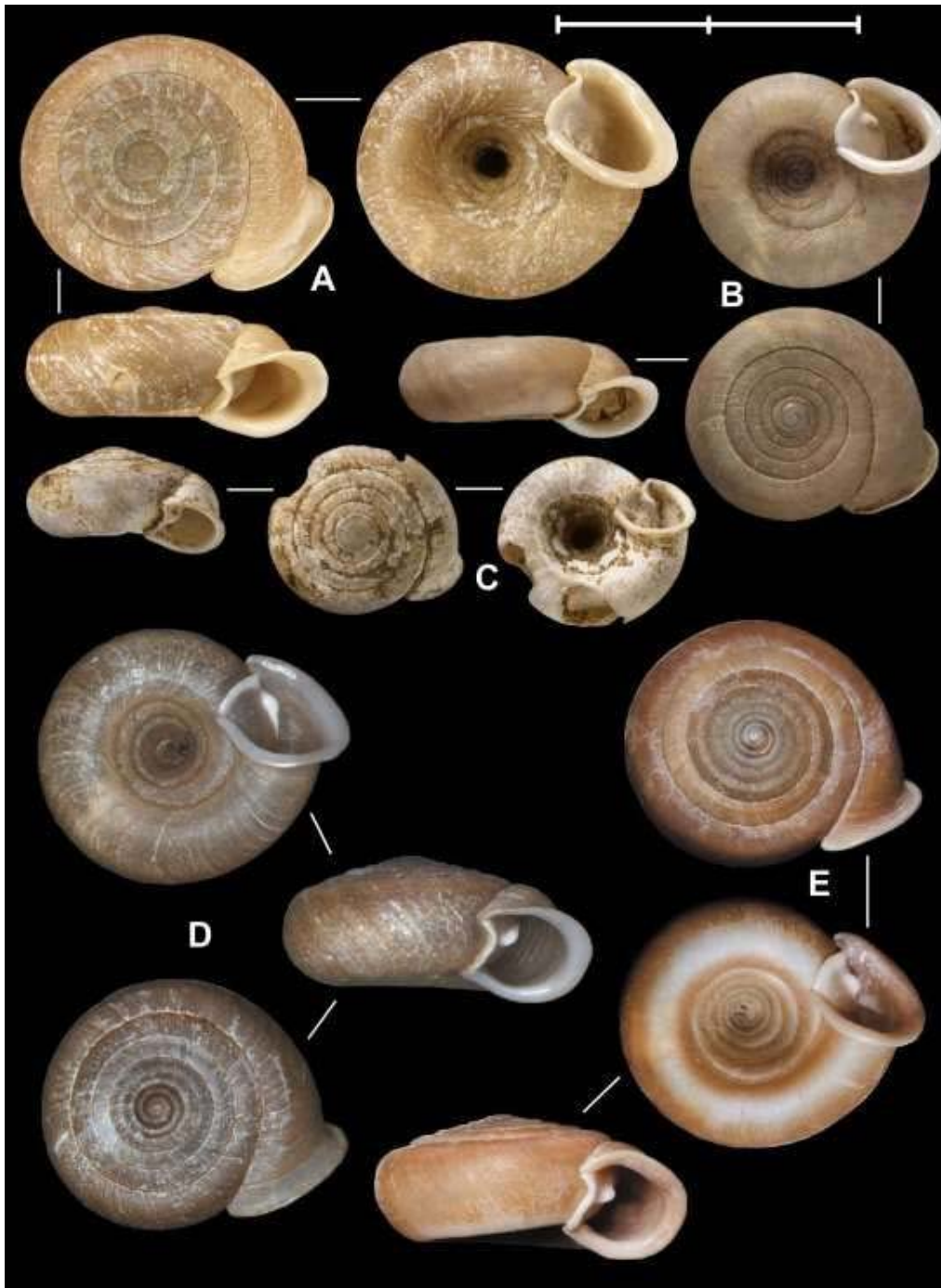


Figure 7.14. A: *Gudeodiscus phlyarius* (typical "fallax var. major"), MNHN-IM-2012-2155, Photos: T. Deli; B: *Gudeodiscus phlyarius*, NHMUK 1922.8.29.58 (holotype of *fallax*), Photos: H. Taylor; C: *Gudeodiscus phlyarius* NHMUK 1922.8.29.55 (holotype of *Plectopylis verecunda*), Photos: H. Taylor; D: *Gudeodiscus phlyarius*, 2009/82, Photos: T. Deli; E: *Gudeodiscus phlyarius* (holotype of *wernerii* Páll-Gergely 2013), HNHM 97438, Photos: T. Deli. Scale represents 20 mm.

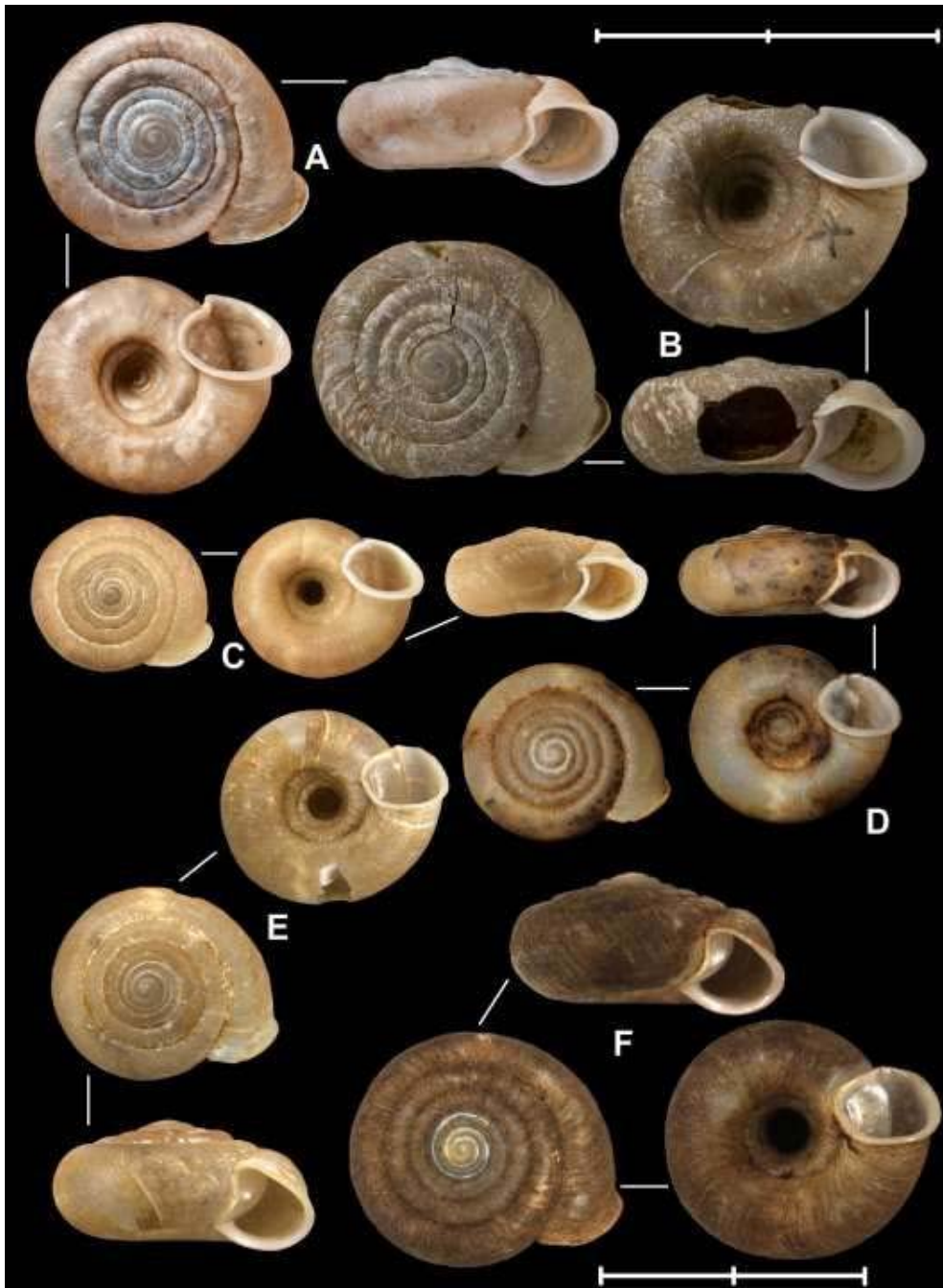


Figure 7.15. A: *Gudeodiscus messengeri raheemi* Páll-Gergely & Hunyadi u. ssp., Vn10-76A, Photos: H. Taylor; B: *Gudeodiscus messengeri messengeri* (Gude 1909), HNMUK 1922.8.29.53 (holotype), Photos: H. Taylor; C: *Gudeodiscus messengeri raheemi* Páll-Gergely & Hunyadi u. ssp., Vn10-76, paratype, Photos: B. Páll-Gergely; D: *Gudeodiscus anceyi* (Gude 1901), MNHN 24600 (syntype), Photos: T. Deli; E: *Gudeodiscus hemmeni* Páll-Gergely & Hunyadi u. sp., HNHM 97458 (holotype), Photos: B. Páll-Gergely; *Gudeodiscus hemmeni* u. sp., Vn10-103A Photos: B. Páll-Gergely. Scales represent 10 mm. Upper scale refers to Figs A–C, and lower scale refers to Figs D–F.

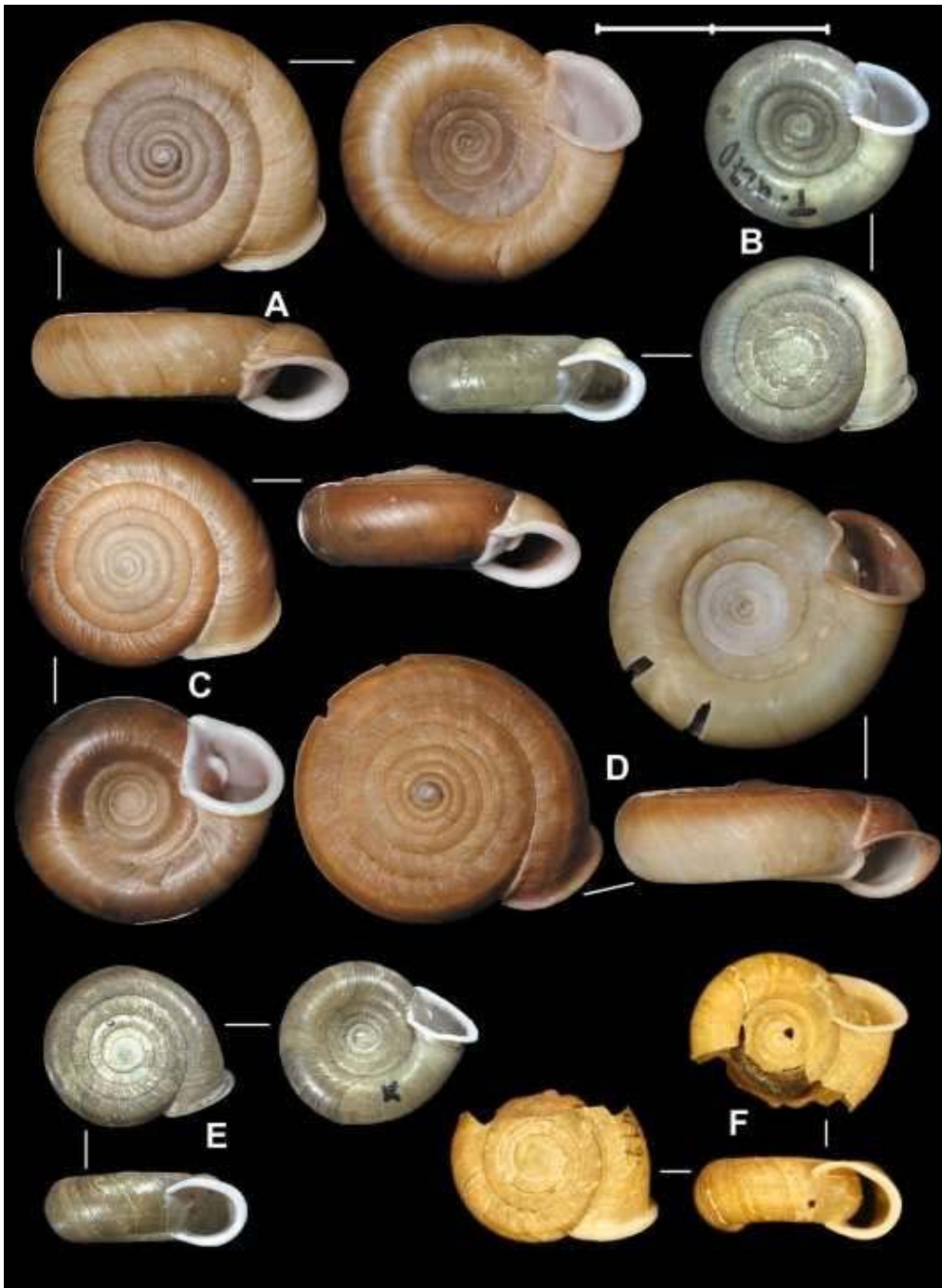


Figure 7.16. A: *Gudeodiscus goliath* Páll-Gergely & Hunyadi 2013, Holotype, HNHM 97442, Photos: T. Deli; B: *Gudeodiscus pulvinaris pulvinaris* (GOULD 1859), Lectotype of *P. pulvinaris continentalis*, SMF 9270, Photos: E. Neubert; C: *Gudeodiscus pulvinaris robustus* Páll-Gergely & Hunyadi 2013., Holotype, HNHM 97439, Photos: T. Deli; D: *G. pulvinaris robustus*, Paratype, HNHM 97440, Photos: T. Deli; E: *Gudeodiscus pulvinaris pulvinaris* (GOULD 1859), SMF 42718, Photos: E. Neubert; *G. pulvinaris pulvinaris*, holotype, MCZ 169316, Photos: A. Baldinger. Scale represents 20 mm.



Figure 7.17. A: *Gudeodiscus marmoreus* Páll-Gergely 2014, holotype, HHNM 97457, Photo, B. Páll-Gergely; B: *Gudeodiscus ursula* Páll-Gergely & Hunyadi 2013., Holotype, HHNM 97454, Photos: J. Harl; C: *Sinicola biforis* (HEUDE 1885), Lectotype, MCZ 167233, Photos: B. Páll-Gergely & J. Harl; D: *Gudeodiscus yanghaoi* Páll-Gergely & Hunyadi 2013, Holotype, HHNM 97441, Photos: T. Deli; E: *Sinicola jugatoria* (Ancey 1885), Syntype (holotype?) NMW.1955.158.24237; F: *Sinicola jugatoria* (Ancey 1885), lectotype of *P. laminiifera*, SMF 9282, Photos: E. Neubert. Scale represents 20 mm.



Figure 7.18. A: *Sinicola fimbriosa* (von Martens 1875), Orig. Hb Pal, Photos: E. Neubert; B: *Sinicola fimbriosa*, Deng2, Photos: B. Páll-Gergely; C: *Sinicola reserata reserata* (Heude 1885), lectotype, MCZ 167130, Photos: B. Páll-Gergely & J. Harl; D: *Sinicola reserata hensanensis* (YEN 1939), holotype, SMF 42814, Photos: E. Neubert; E: *Sinicola reserata azona* (Gredler 1887), lectotype, NHMW 31727, Photos: J. HARL; F: *Sinicola schmackeri* Páll-Gergely 2013, Holotype, SMF 42706, Photos: E. Neubert. Scale represents 10 mm.



Figure 7.19. A: *Sinicola vargabalinti* Páll-Gergely 2014, holotype, HNHM 97455, Photos: B. Páll-Gergely; B: *S. vargabalinti*, same data, HNHM 97456 (paratype), Photos: B. Páll-Gergely; C: *Sinicola stenochila stenochila* (Möllendorff 1885), lectotype, SMF 9267, Photos: E. Neubert; D: *Sinicola stenomphala* Páll-Gergely & Hunyadi 2013, holotype, HNHM 97453, Photos: J. HARL; E: *Sinicola alphonsi* (Deshayes 1870), syntype (holotype?), NHMP 24717, Photos: Ph. Maestrati; F: *Sinicola stenochila basilia* GÜDE, 1897, syntype, NHMUK 1922.8.29.97, Photos: H. Taylor & Ph. Hurst. Scale represents 10 mm.



Figure 7.20. A: *Sinicola murata* (HEUDE 1885), 20070710B, Photos: J. HARL; B: *Sinicola emoriens* (Gredler 1881), syntype, NHMW, Photos: J. Harl; C: *Sinicola asamiana* Páll-Gergely 2013, holotype, HNHM 97452, Photos: J. Harl; D: *Sinicola straeleni* (Yen 1937), Paratype, RBINS 8B/9/f1, Photos: J. Harl; E: *Sicradiscus cutisculpta* (Möllendorff 1882), lectotype, SMF 9265, Photos: E. Neubert; F: *Sicradiscus diptychia* (Möllendorff 1885), lectotype, SMF 9272, Photos: E. Neubert. Scale represents 10 mm.



Figure 7.21. A: *Sicradiscus securus* (Heude 1889), Syntype, MCZ 167129, Photos: J. Harl; B: *Sicradiscus feheri* Páll-Gergely & Hunyadi, 2013, holotype, HNHM 97444, Photos: J. Harl; C: *Sicradiscus schistoptychia* (Möllendorff 1886), lectotype, SMF 9263, Photos: E. Neubert; D: *Sicradiscus transitus* Páll-Gergely 2013, holotype, HNHM 97485, Photos: B. Páll-Gergely; E: *Sicradiscus invius* (Heude 1885), lectotype, USNM 472167, Photos: J. Harl; F: *S. invius*, 20070708B, Photos: J. Harl. Scale represents 10 mm.

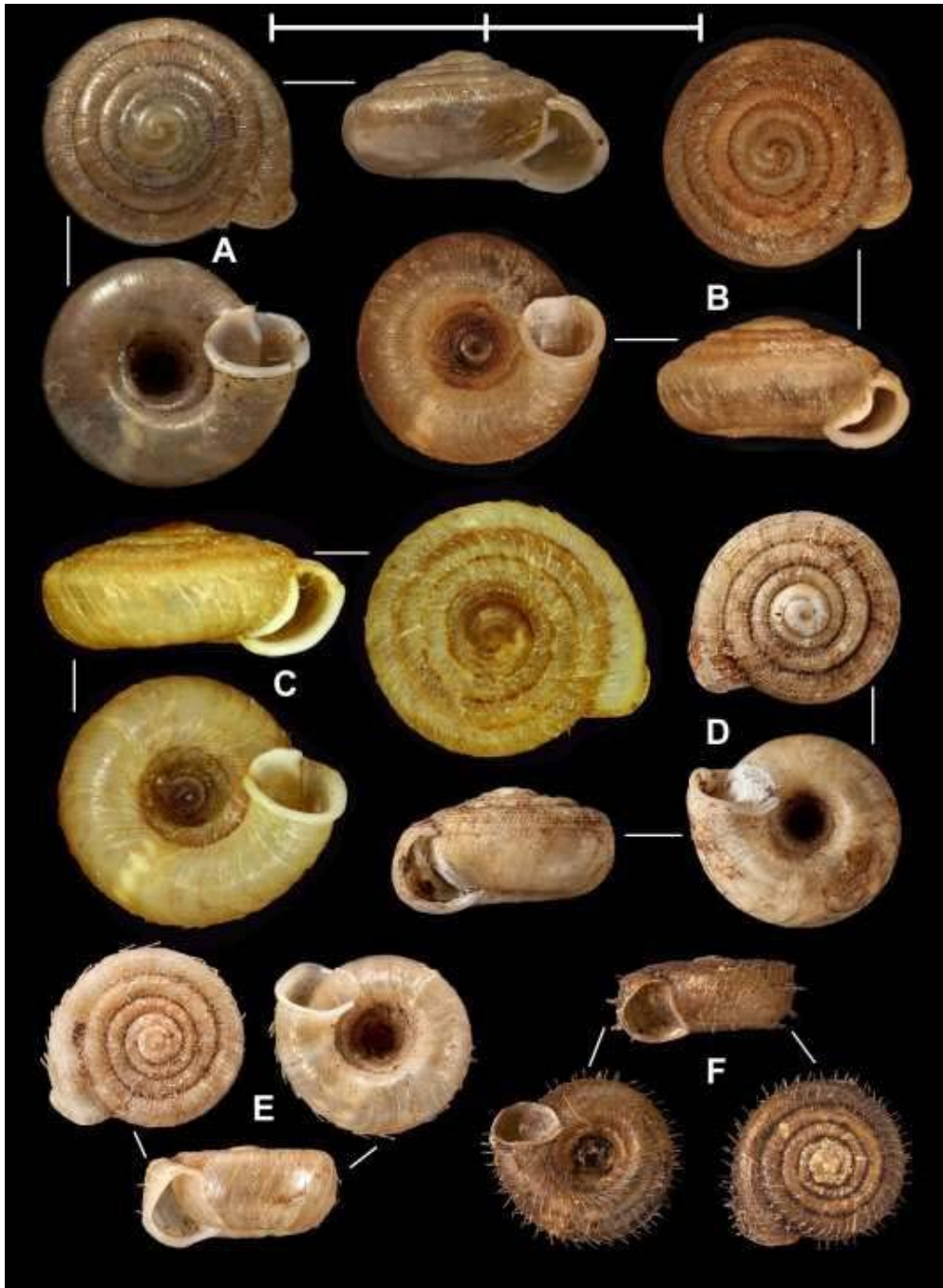


Figure 7.22. A: *Sicradiscus mansuyi* (Gude 1908), syntype, NHMUK 1907.2.20.19., Photos: H. Taylor; B: *Sicradiscus hirasei* (Pilsbry 1904), lectotype, ANSP 87632, Photos: F. Borrero; C: *Sicradiscus ishizakii* (Kuroda 1941), paratype, NCP 244, Photo used with permission from Hwang et al 2008; D: *Endothyrella* species 7, u. sp., Photos: H. Taylor; E: *Endothyrella nomennovum* 1 (nom. nov. pro *minor* Godwin-Austen 1879), probably syntype, NHMUK 1891.3.17.358-359., Photos: H. Taylor; F: *Endothyrella nomennovum* 1, Nepal, Phulchowki hill, Photos: H. Taylor. Scale represents 10 mm.

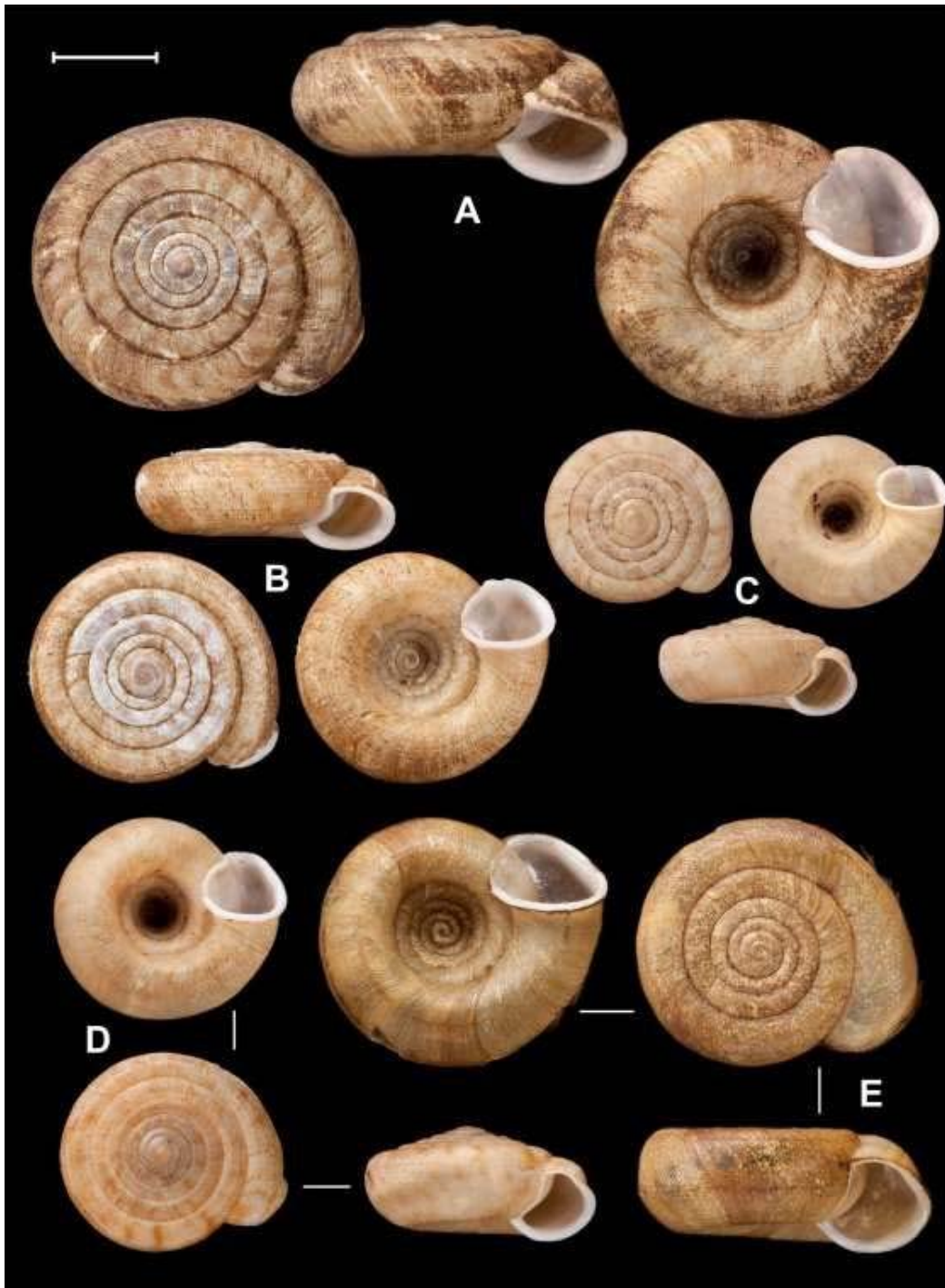


Figure 7.23. A: *Endothyrella oglei* (Godwin-Austen, 1879), syntype, NHMUK 1903.7.1.740.; B: *Endothyrella serica* (Godwin-Austen, 1875), NHMUK 1903.7.1.741; C: *Endothyrella serica* (Godwin-Austen, 1875), syntype of *serica*, NHMUK 1903.7.1.744.; D: *Endothyrella serica* (Godwin-Austen, 1875), syntype of *munipurensis*, NHMUK 1903.7.1.742.; E: *Endothyrella babbagei* (Gude 1915), holotype, NHMUK 1903.7.1.3529. All Photos by H. Taylor. Scale represents 10 mm.

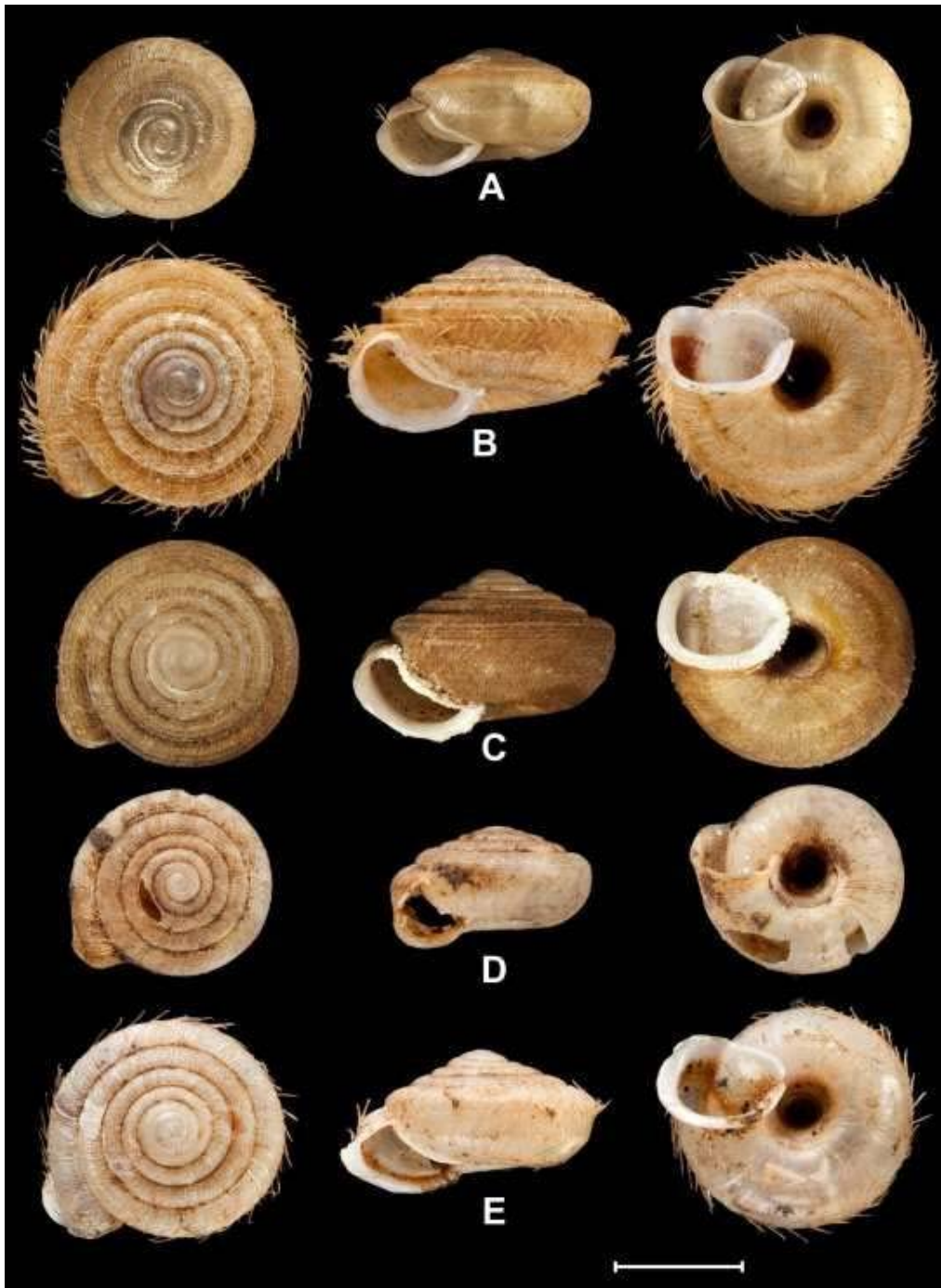


Figure 7.24. A: *Endothyrella plectostoma* (Benson 1836), syntype, UMZC 102155; Photos: Jamie Gundry; B: *Endothyrella plectostoma exerta* (Gude 1901), holotype, NHMUK 1922.8.29.50., Photos: Harold Taylor; C: *Endothyrella plectostoma tricarinata* (Gude 1896), syntype, UMZC 102170., Photos: Jamie Gundry; D: *Endothyrella sowerbyi* (Gude 1898), holotype, NHMUK 1922.8.29.48., Photos: Harold Taylor; E: *Endothyrella affinis* (Gude 1897), holotype, NHMUK 1922.8.29.26, Photos: Harold Taylor. Scale represents 10 mm.

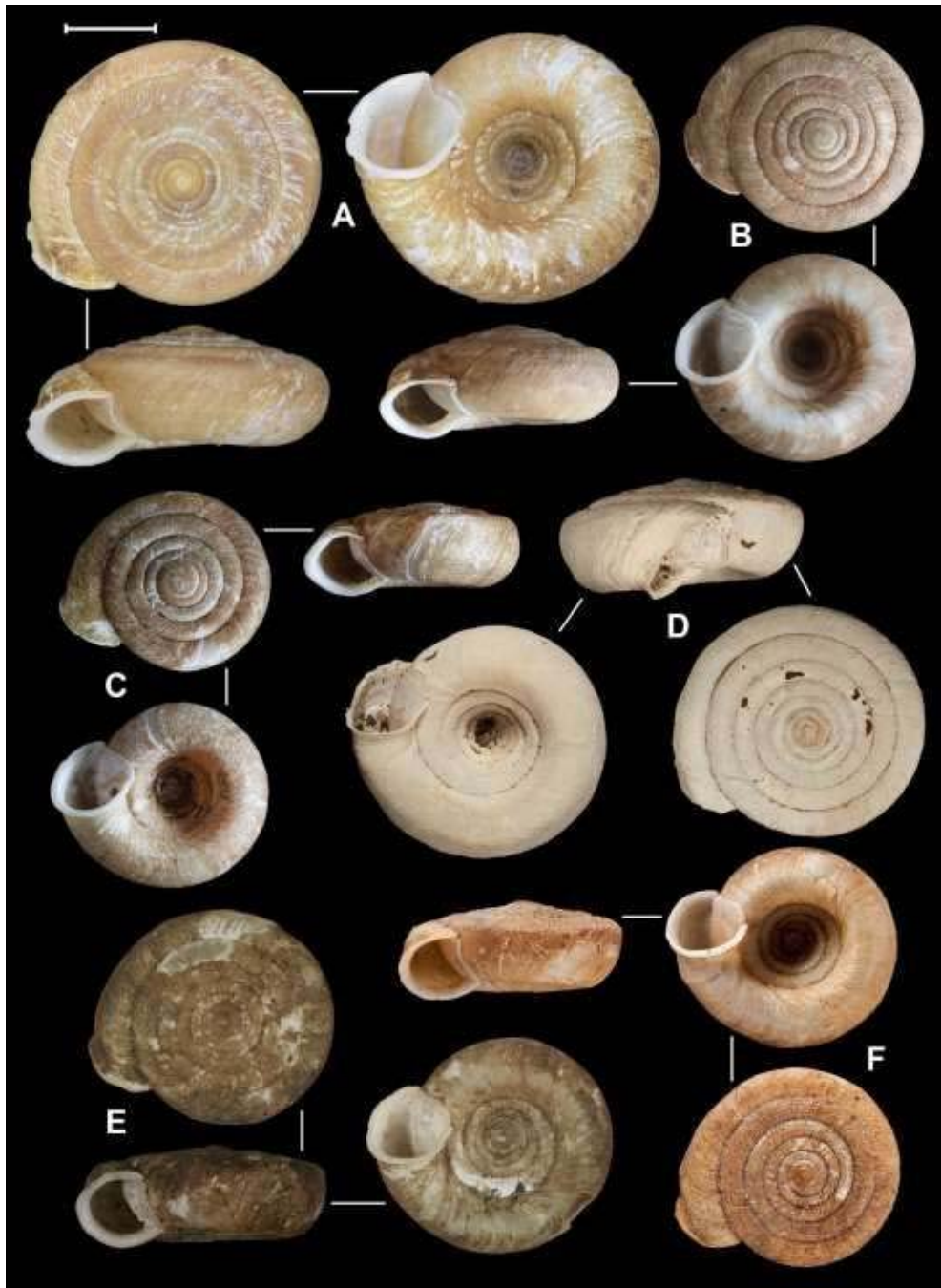


Figure 7.25. A: *Endothyrella* species8 u. sp., CDZMTU004, Photos: B. Páll-Gergely; B: *Endothyrella* species8 u. sp., (holotype), Photos: E. Bochud; C: *Endothyrella* species8 u. sp., paratype, NMBE 527538, Photos: E. Bochud; D: *Endothyrella pinacis* (Benson 1859), Sikkim, coll. Benson, UMZC 102755 (holotype of *pinacis*), Photos: Jamie Gundry; E: *Endothyrella pinacis* (Benson 1859), holotype of *Helix pettos*, ZMB/MOLL 17905, Photos: Christine Zorn; F: *Endothyrella pinacis* (Benson 1859), NHMUK 1906.2.2.143., Photos: Harold Taylor. Scale represents 5 mm.

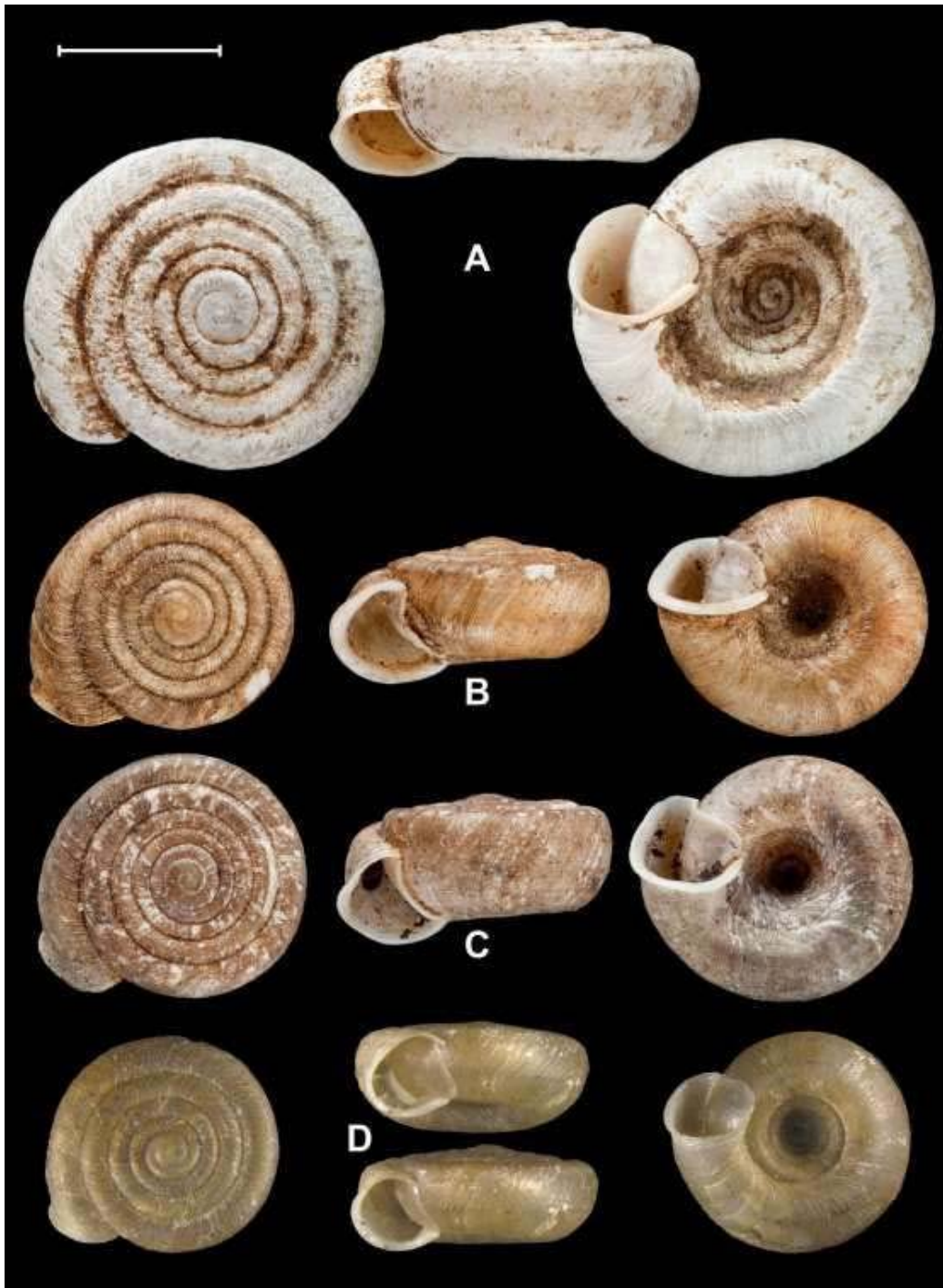


Figure 7.26. A: *Endothyrella oakesi* (Gude 1915), syntype, NHMUK 1903.7.1.3125., Harold Taylor; B: *Endothyrella brahma* (Godwin-Austen 1879), syntype, NHMUK 1903.7.1.751., Photos: Harold Taylor; C: *Endothyrella bedfordi* (Gude 1915), syntype, NHMUK 1903.7.1.3584., Photos: Harold Taylor; D: *Endothyrella* species4 u. sp., holotype, CDZMTU018, Photos: E. Bochud. Scale represents 5 mm.

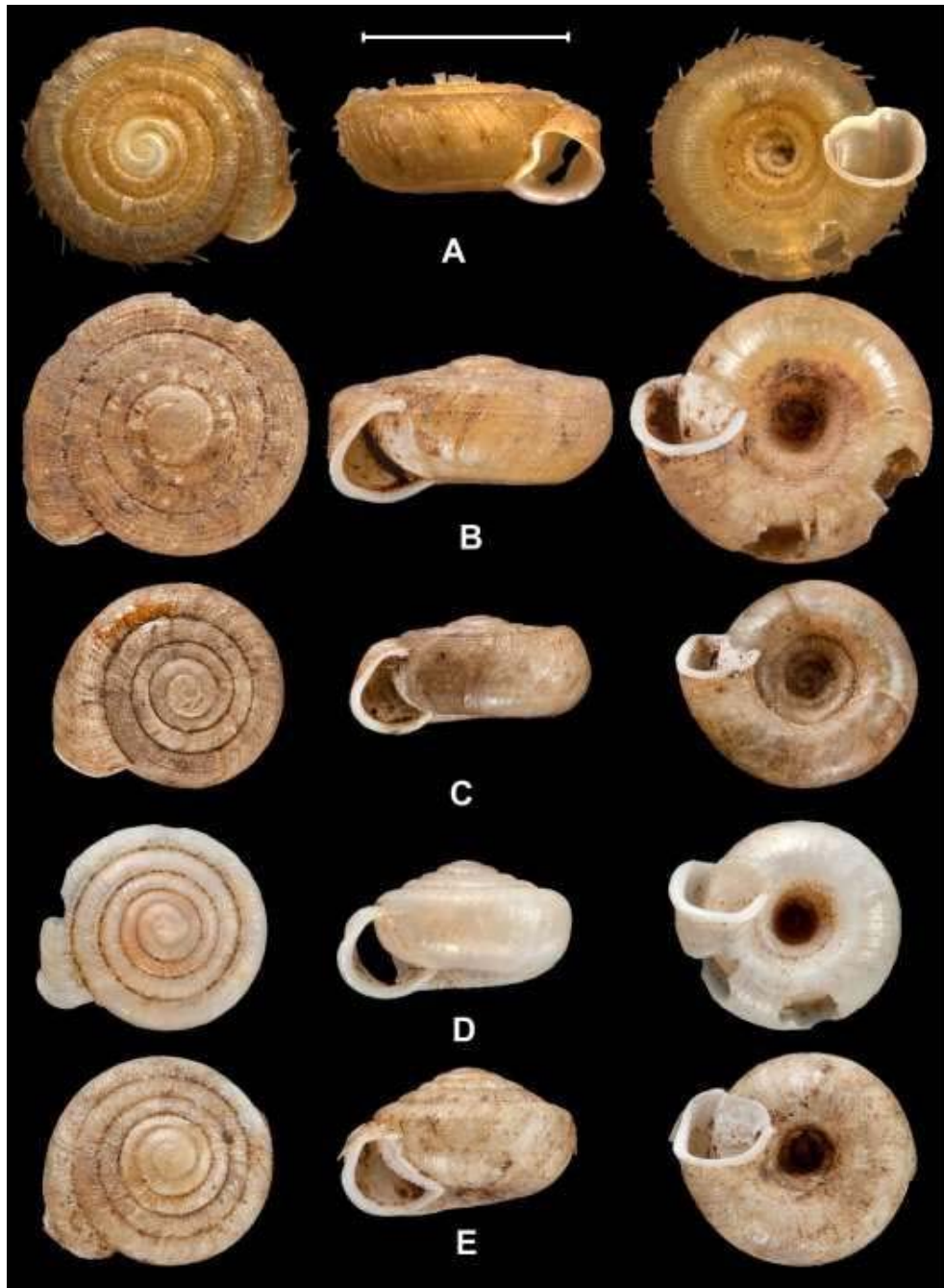


Figure 7.27. A: *Endothyrella* species6, u. sp., holotype, NHMUK 20140023, Photos: B. Páll-Gergely; B: *Endothyrella macromphalus gregorsoni* (Gude 1915), holotype, NHMUK 1903.7.1.3124., Photos: Harold Taylor; C: *Endothyrella macromphalus macromphalus* (W. Blandford 1870), holotype, NHMUK 1906.1.1.754., Photos: Harold Taylor; D: *Endothyrella blanda* (Gude 1898), holotype, NHMUK 1922.8.29.41., Photos: Harold Taylor; E: *Endothyrella williamsoni* (Gude 1915), holotype, NHMUK 1903.7.1.3087., Photos: Harold Taylor. Scale represents 5 mm.

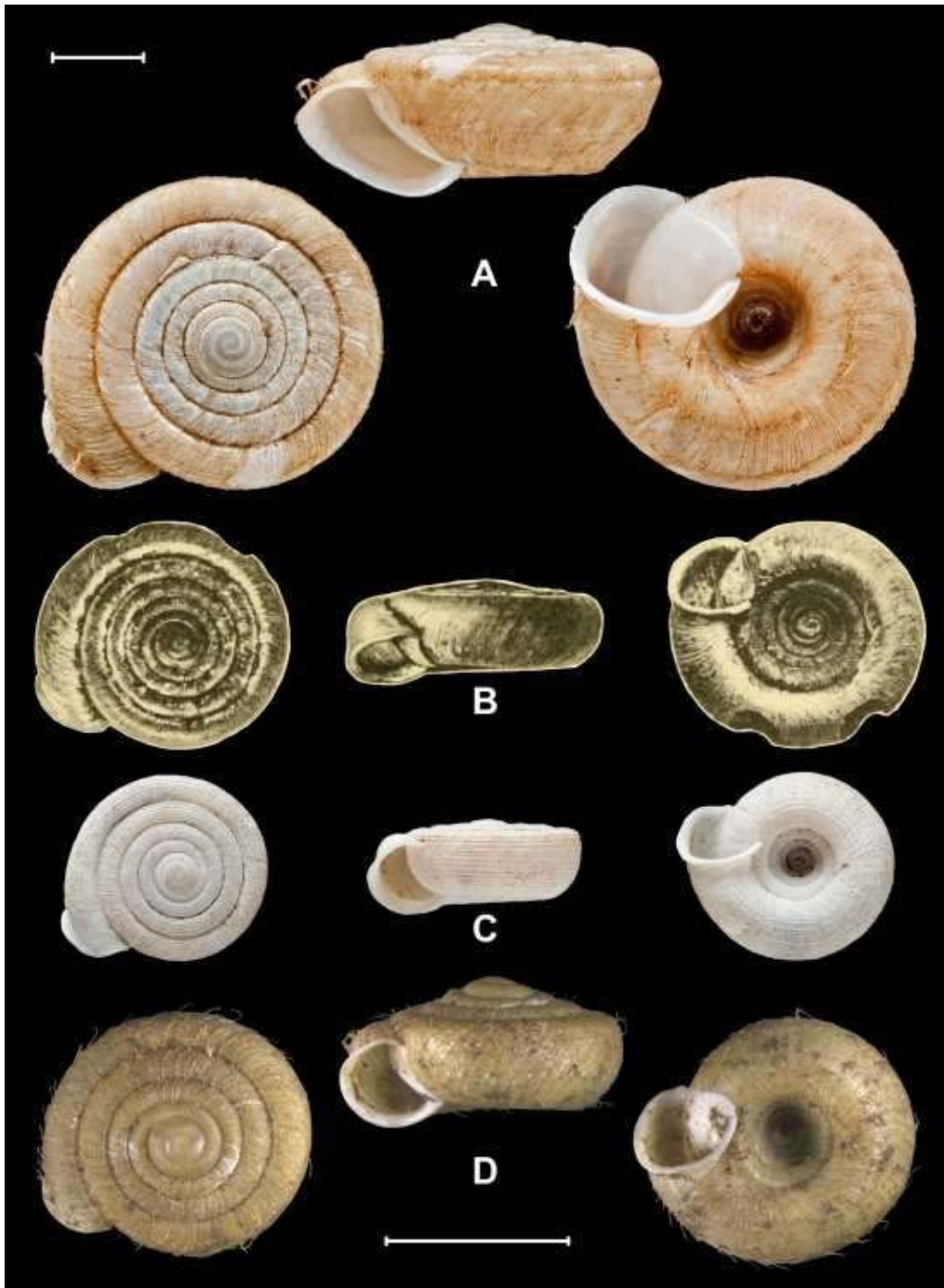


Figure 7.28. A: *Endothyrella fultoni* (Godwin-Austen 1892), syntype, NHMUK 1903.7.1.301. Photos: H. Taylor; B: *Endothyrella aborensis* (Gude 1915), holotype, photos published in Gude (1915), Photos from the original publication; C: *Endothyrella miriensis* (Gude 1915), NHMUK 1903.7.1.3205. (syntype), Photos: H. Taylor; D: *Endothyrella* species5, u. sp., CDZMTU001 (holotype), Photos: E. Bochud.

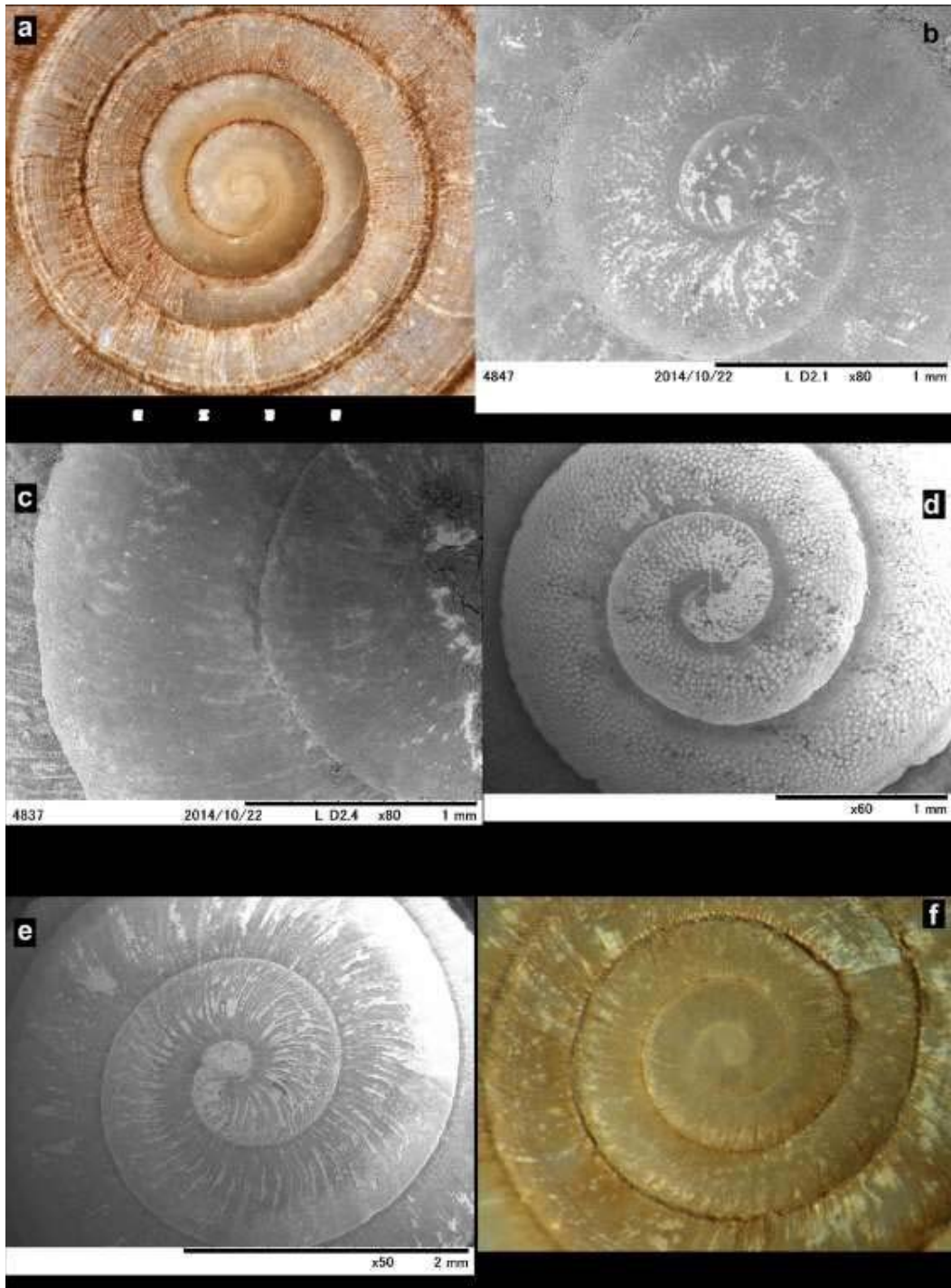


Figure 7.29. Protoconchs of Plectopylidae species. A: Genus1 (?) *austeni* Gude, 1899 syntype; B: Genus1 *dextrorsa* UF 76385; C: *Plectopylis* species2, 2013/14; D: *Chersaecia shanensis* (Stoliczka 1873), Myanmar, Shan, Kalaw, Shwe U Min Cave, 1340 m, E: *Plectopylis bensoni* Gude 1914, Myanmar, Kayin, East foot of Zwegabin Mt., Pha-an, F: *Plectopylis lintera* Möllendorff 1897, lectotype. All photos B. Páll-Gergely, except for Figure 7.29A (H. Taylor).

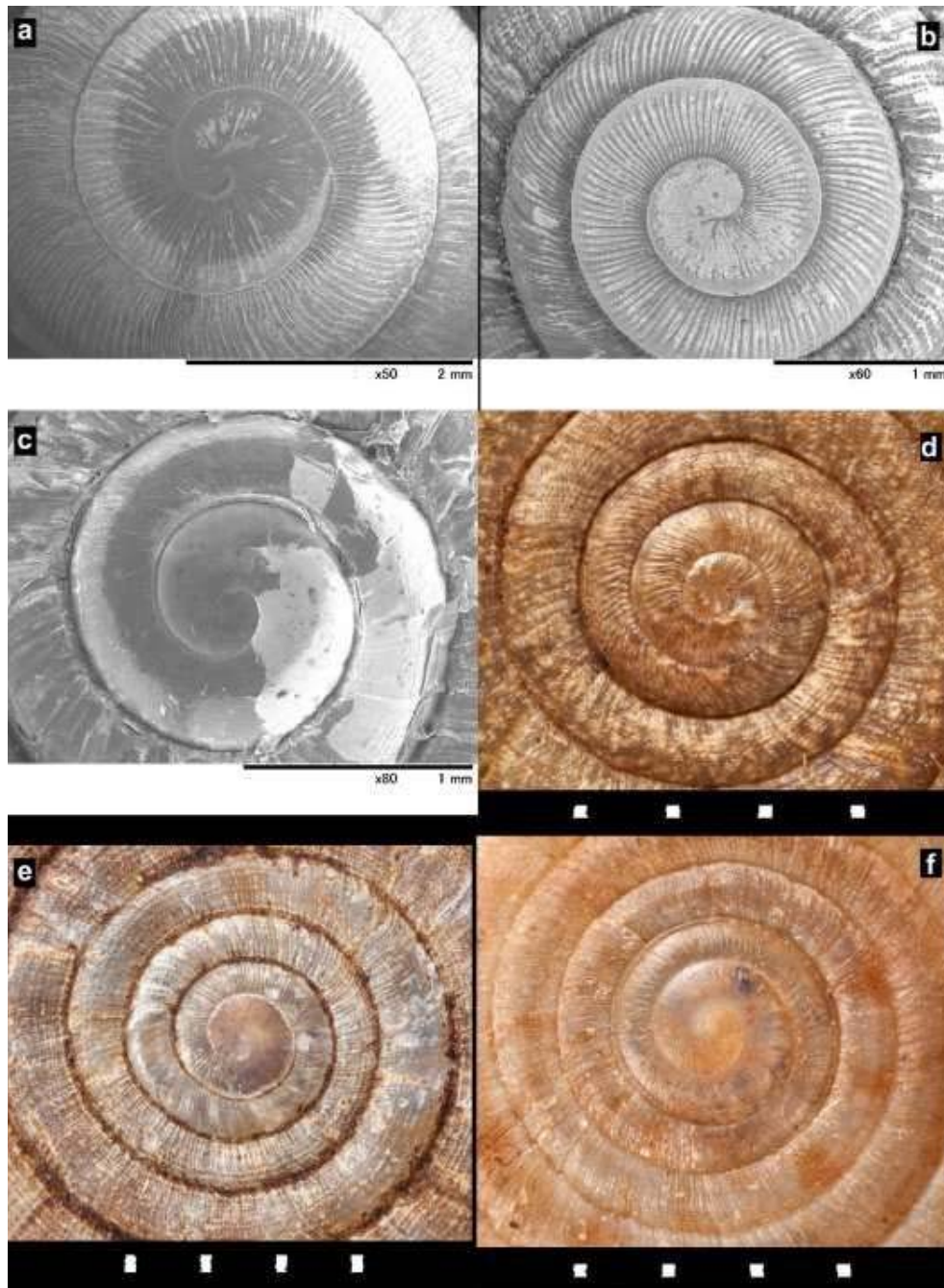


Figure 7.30. Protoconchs of Plectopylidae species. A: Genus3 *laomontana* (L. Pfeiffer 1862), Laos, Luang Prabang Province, Ban Pak Ou, Nam Wu (opposite side of Ban Pak Ou); B: *Endothyrella* species8 u. sp., PL002; C: *Endothyrella* species6, u. sp., holotype; D: *Endothyrella babbagei* (Gude 1915), holotype, E: *Endothyrella oglei* (Godwin-Austen, 1879), NHMUK 1903.7.1.740. (syntype); F: *Endothyrella serica* (Godwin-Austen, 1875), NHMUK 1903.7.1.742. (syntype of *munipurensis*). Image A–C: B. Páll-Gergely, D–F: H. Taylor.

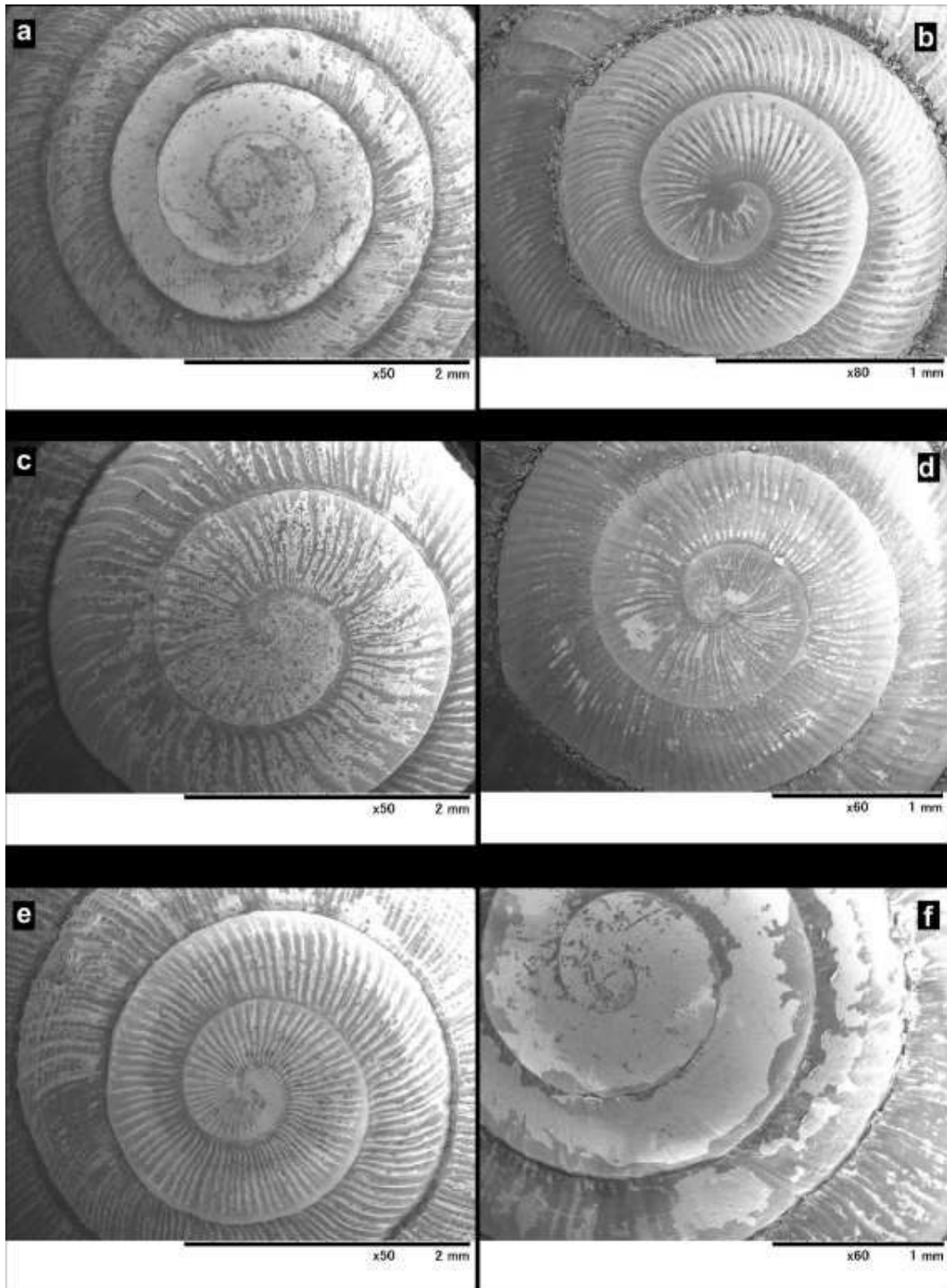


Figure 7.31. Protoconchs of Plectopylidae species. A: *Sicradiscus schistoptychia* (Möllendorff 1886), 2010/48; B: *Sinicola stenochila stenochila* (Möllendorff 1885), 2010/30; C: *Sinicola fimbriosa* (von Martens 1875), Deng2; D: *Gudeodiscus messengeri raheemi* Páll-Gergely & Hunyadi u. ssp., Vn11-104A; E: *Gudeodiscus* (*G.*) *villedaryi* (Ancey 1888), Vn11-163. All images: B. Páll-Gergely.

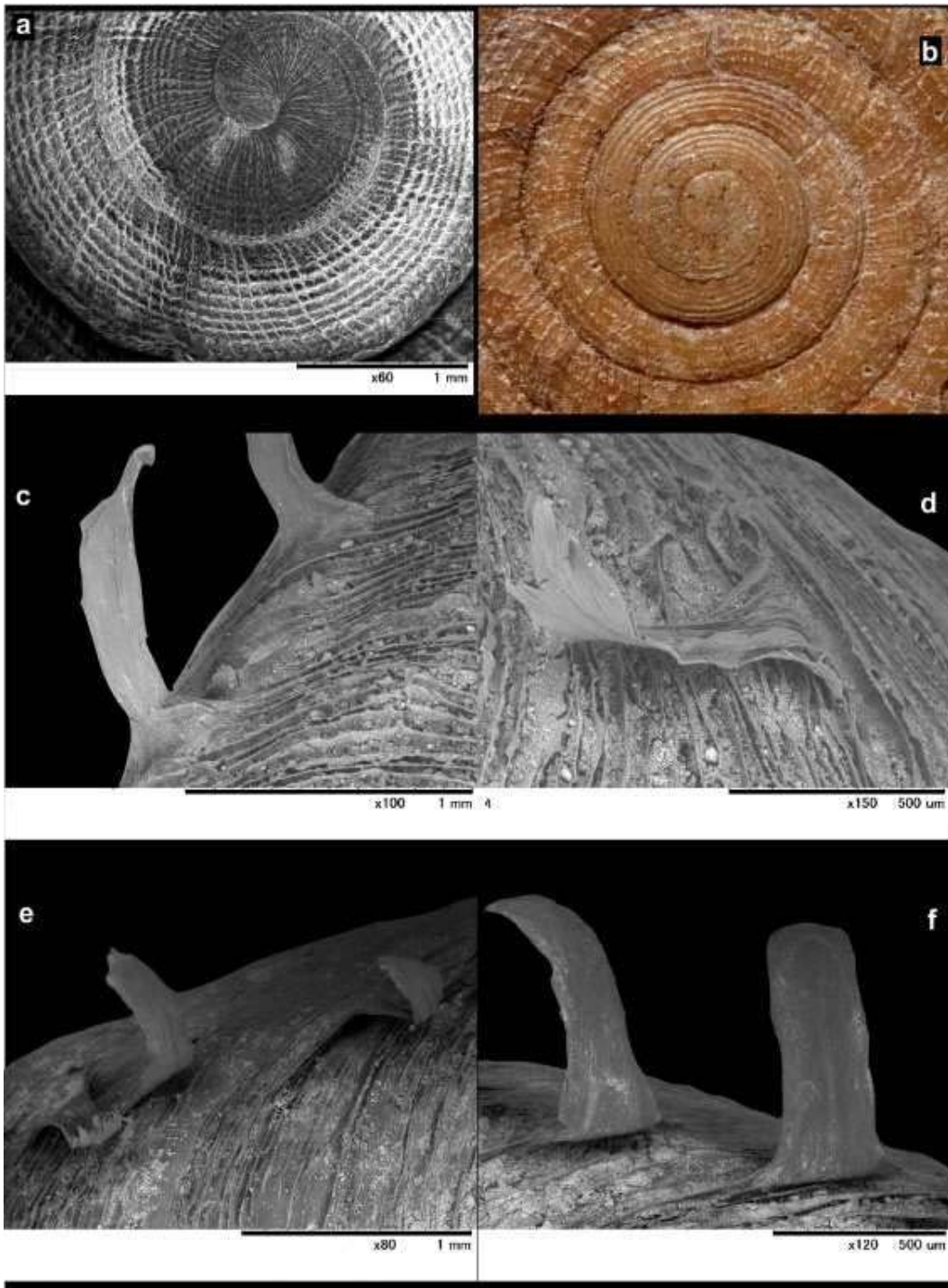


Figure 7.32. Protoconchs and periostracum filaments of Plectopylidae species. A: Genus2 species3 u. sp. paratype; B: Genus2 *andersoni* (W. BLANFORD 1869), NHMUK 20130003; C–D: Genus1 *dextrorsa*, NHMUK 1901.4.2.10; E–F: *Plectopylis* species2, 2013/14. All images B. Páll-Gergely except for Figure B (H. Taylor).

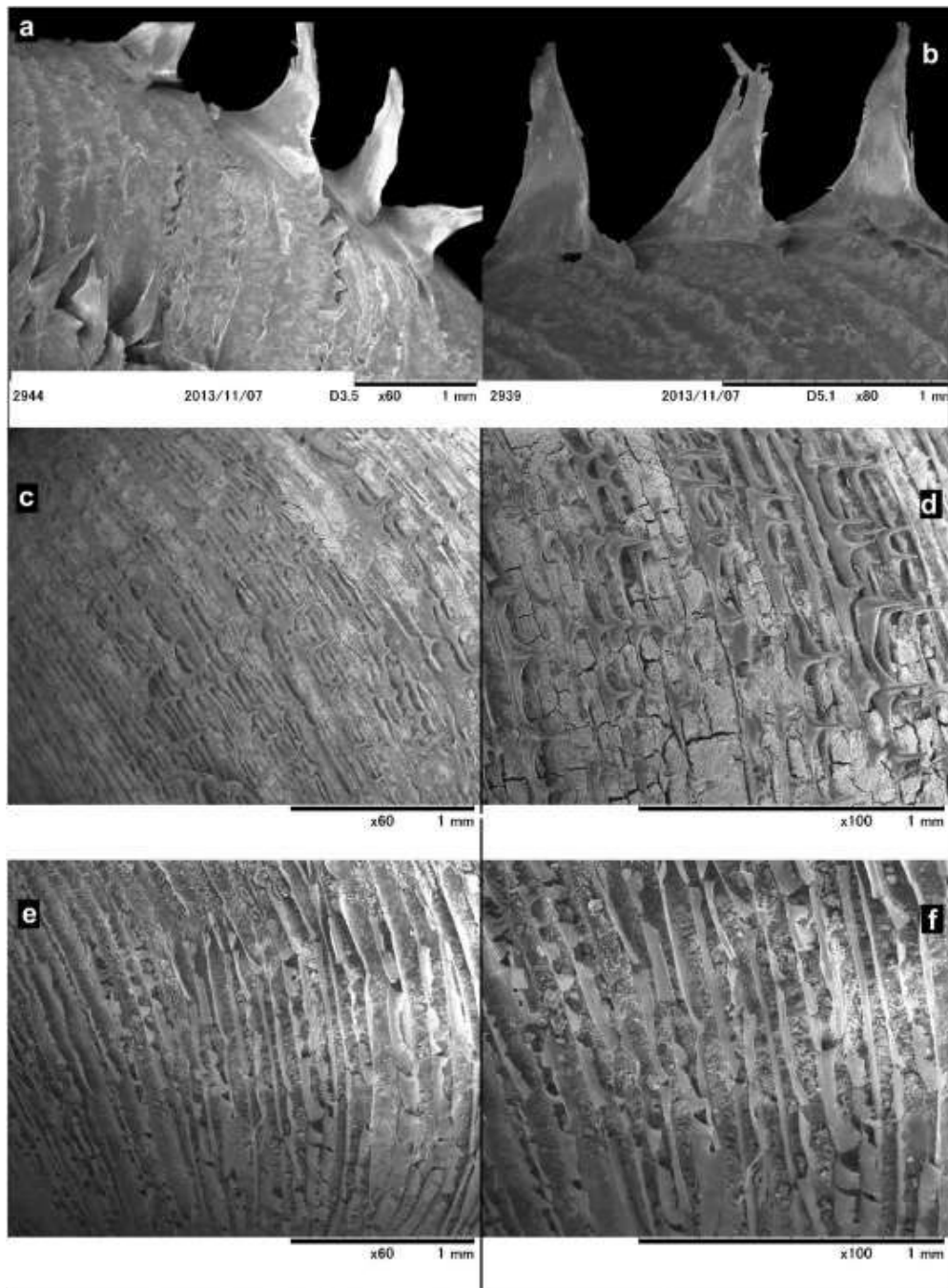


Figure 7.33. Periostracum filaments of Plectopylidae species. A–B: *Sinicola vargabalinti*, paratype, HNHM 97456; C–D: sculpture of *G. (G.) phlyarius* (Mabille 1887), Vn10-56, coll. HE; E–F: sculpture of *G. (G.) phlyarius* (Gude 1909) (typical *fallax* specimen), Vn11-187, coll HE. Images: B. Páll-Gergely.

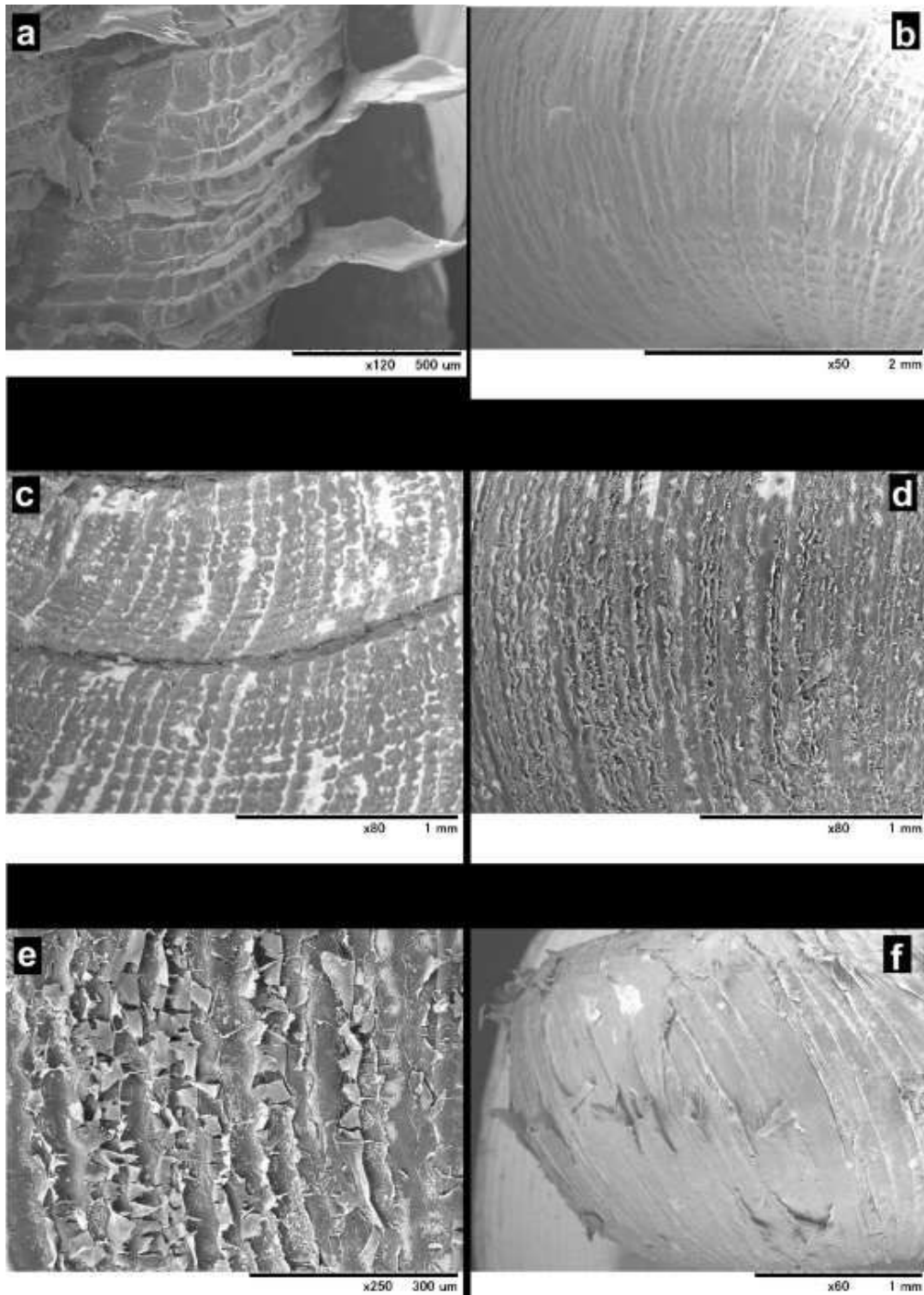


Figure 7.34. Periostracum filaments and shell sculpture of Plectopylidae species. A: *Sinicola stenochila*; B: *Endothyrella plectostoma* (Benson 1836), body whorl, Shwegoo, Birmania, leg. Mission L. Fea 1885–1889; C: *Endothyrella species8* Budha & Páll-Gergely n. sp, 4th, 5th whorl; D: *Endothyrella species8* u. sp. body whorl; E: *Endothyrella species8* u. sp. body whorl; F: *Endothyrella species6*, u. sp., body whorl NHMUK 20140023. All images: B. Páll-Gergely.

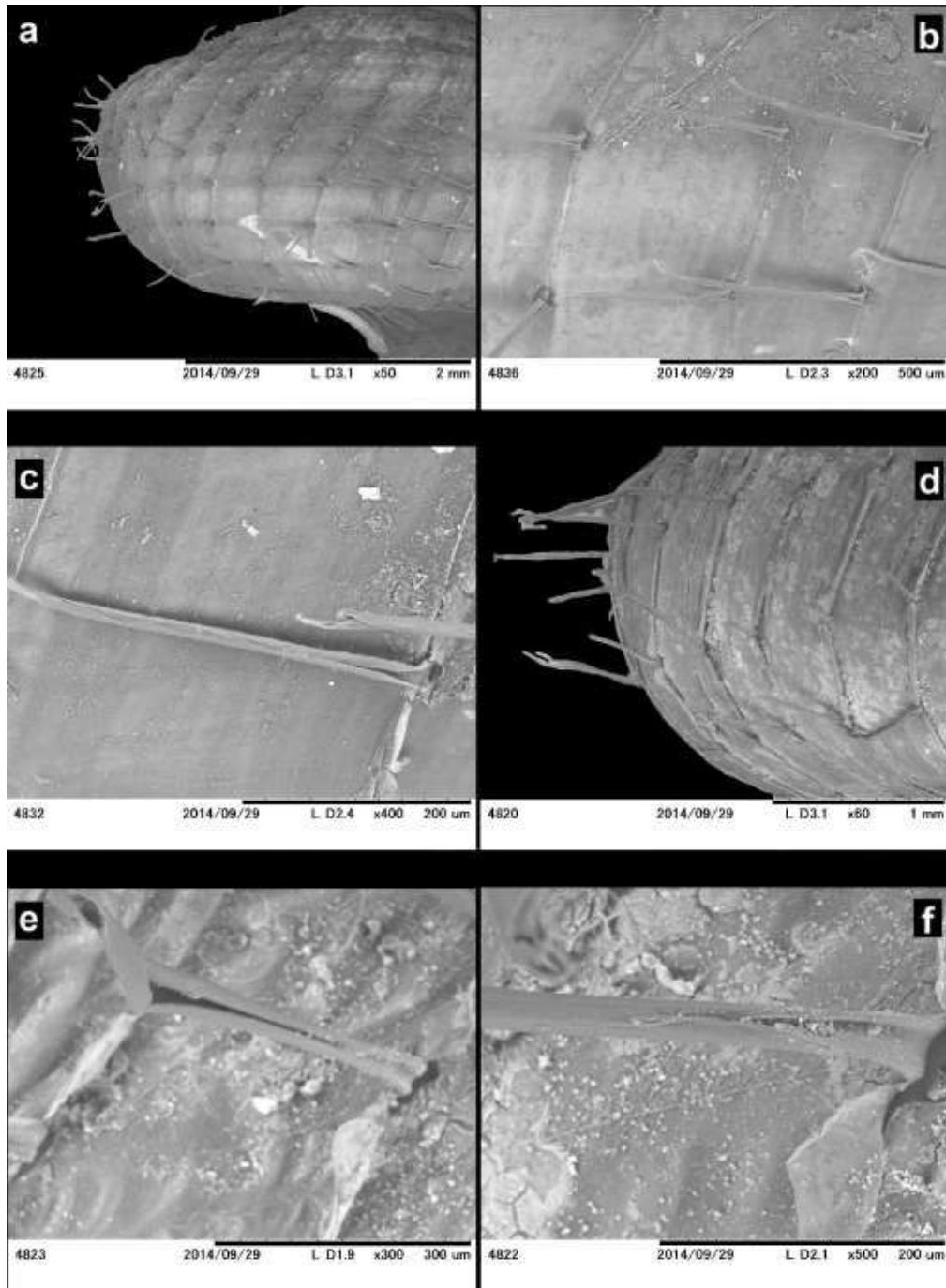


Figure 7.35. Periostracum filaments and shell sculpture of Plectopylidae species. A–C: *Endothyrella blanda* (Gude 1898), Silchar Cachar, F. Ede, coll. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.502.; D–F: *Endothyrella plectostoma* (Benson 1836), Sikkim, leg. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.451. All images: B. Páll-Gergely.

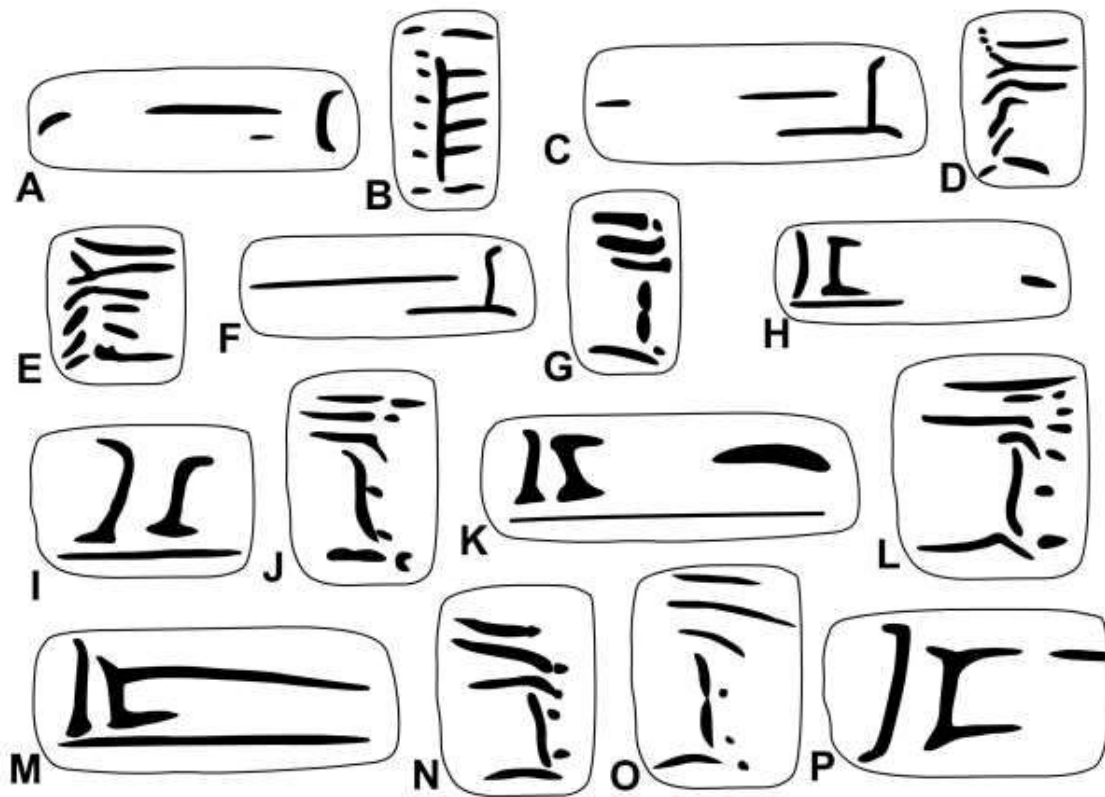


Figure 7.36. Parietal (A, C, F, H, I, K, M, P) and palatal (B, D, E, G, J, L, N, O) plication of Genus1 and *Chersaecia* species. A–B: Genus1 *austeni* (after Gude 1899c); C–D: Genus1 *dextrorsa* Benson 1860 (*Plectopylis brachydiscus*, after Gude 1896c); E–F: Genus1 *dextrorsa* Benson 1860 (after Gude 1896c); G–H: *Chersaecia feddeni* (*Plectopylis ponsonbyi*, after Gude 1896d); I–J: *Ch. feddeni* (*Plectopylis lissochlamys*, after Gude 1914b); K–L: *Ch. feddeni* (*Plectopylis magna*, after Gude 1914b); M–N: *Ch. feddeni* (*Plectopylis leucochila* after Gude 1914b); O–P: *Ch. feddeni* (after Gude 1914b). All palatal plicae are shown from inner view.

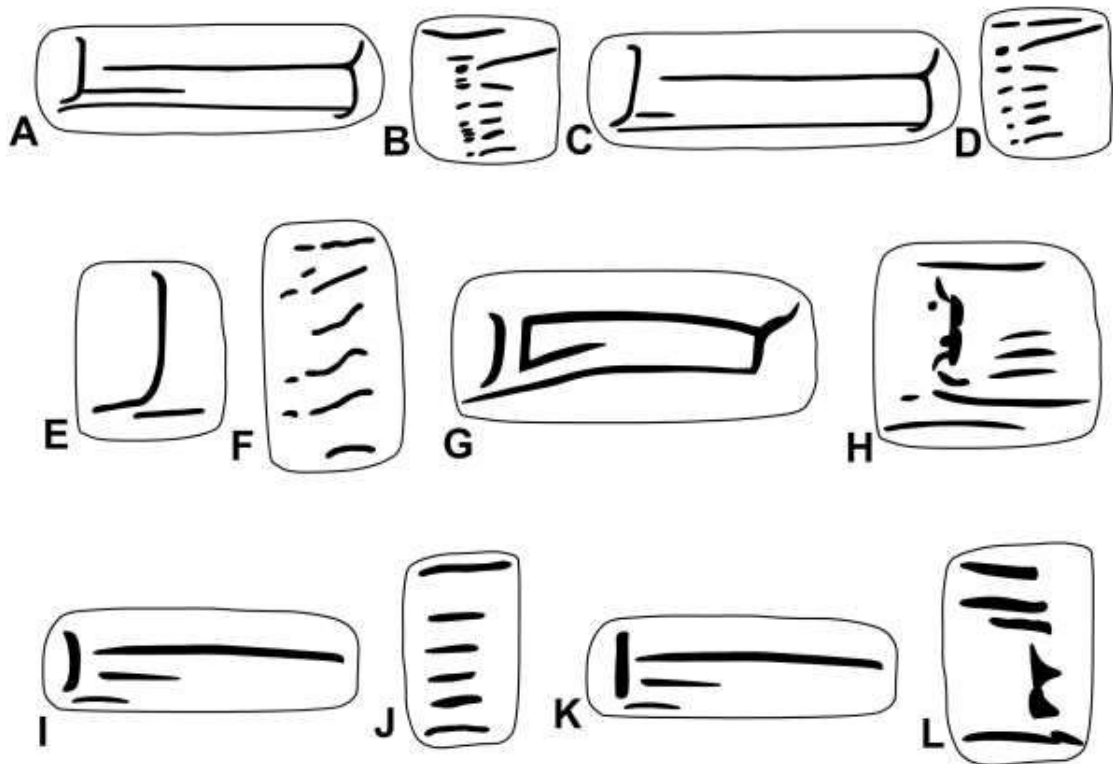


Figure 7.37. A–B: Parietal (A, C, E, G, J, K) and palatal (B, D, F, H, J, L) plication of *Chersaecia* taxa. *Chersaecia shanensis* (Stoliczka 1873) from Myanmar, Shan, Kalaw, Shwe U Min Cave, C–D: *Chersaecia shanensis* (Stoliczka 1873) from Myanmar, Shan, in the suburbs of Kalaw, Myin Mahti Cave; E–F: *Chersaecia* species1, holotype, NHMUK; G–H: *Ch. woodthorpei* (after Gude 1914b); I–J: *Chersaecia perarcta* (after Gude 1896c); K–L: *Chersaecia shiroiensis* (after Gude 1896c). Inner views: H, J, L; outer views: B, D, F.

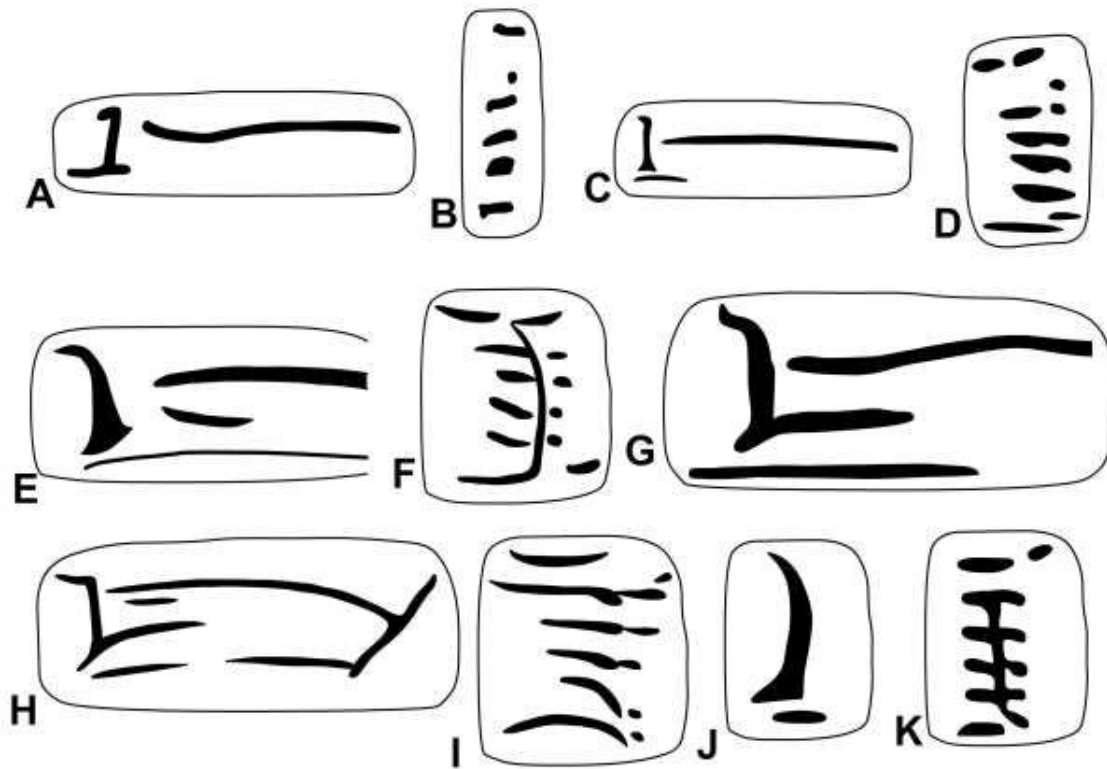


Figure 7.38. A–B: Parietal (A, C, E, G, H, J) and palatal (B, D, F, I, K) plication of *Chersaecia* taxa. A–B: *Chersaecia shiroiensis* subspecies1 u. ssp., holotype, NHMUK; C–D: *Chersaecia refuga* (*Plectopylis nagaensis*, after Gude 1897a); E–F: *Chersaecia refuga* (*Plectopylis kengtungensis*, after Gude 1914b); G: *Chersaecia refuga* (*Plectopylis pseudophis*, after Gude 1914b); H–I: *Chersaecia refuga* (*Plectopylis leiophis*, after Gude 1914b); J–K: *Ch. refuga muspratti* (after Gude 1914b). Inner views: D, F, I, K; outer view: B.

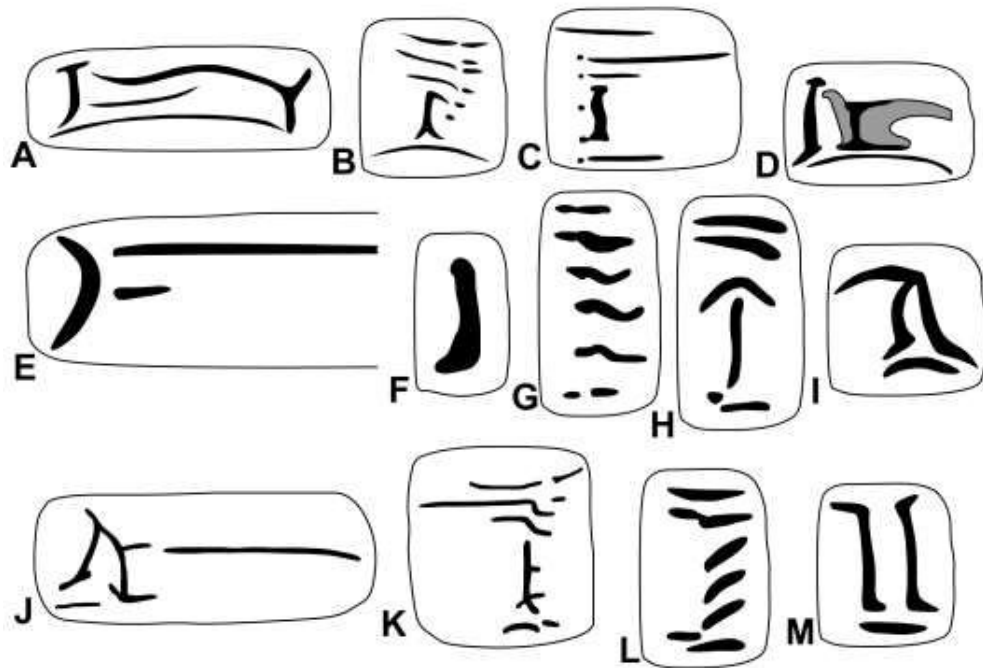


Figure 7.39. Parietal (A, D, E, F, I, J, M) and palatal (B, C, E, G, H, K, L) plication of *Chersaecia* and *Plectopylis* taxa. A–B: *Chersaecia perrierae* (after Gude 1914b); C–D: *Chersaecia goniobathmos* (Ehrmann 1922), after the orig. description; E: *Chersaecia refuga* (after the orig. description of *P. degerbolae* Solem 1966); F–G: *Ch. perarcta simplex* (Solem, 1966), after the orig. description; H–I: *Plectopylis cyclaspis* (after Gude 1914b); J–K: *Plectopylis* species2 u. sp., paratype; L–M: *Endoplon brachyplecta* (after Gude 1914b). Inner views: B, G, H, K, L; outer view: C.

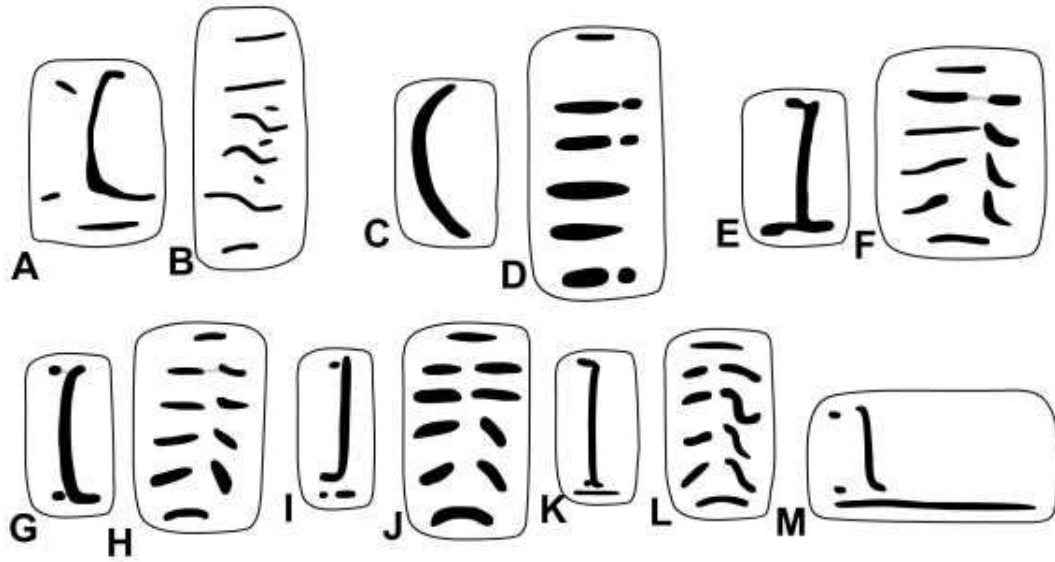


Figure 7.40. Parietal (A, C, E, G, I, K, M) and palatal (B, D, F, H, J, L) plication of *Endoplion* and *Endothyrella* taxa. A–B: *Endoplion smithiana*, NHMUK 1888.12.4.1555–1556 (two different specimens); C–D: *Endothyrella* species6 u. sp. (NHMUK 20140023, holotype); E–F: *Endothyrella* species8 u. sp. PL004, paratype; G–H: *Endothyrella* species8 u. sp. PL008, paratype; I–J: *Endothyrella* species5 u. sp. PL002, paratype; K–L: *Endothyrella* species4 sp. PL001, paratype; M: *Endothyrella* species7 u. sp. (after Gude 1914b, under the name *minor*). Inner views: F, H, J, L; outer views: B, D.

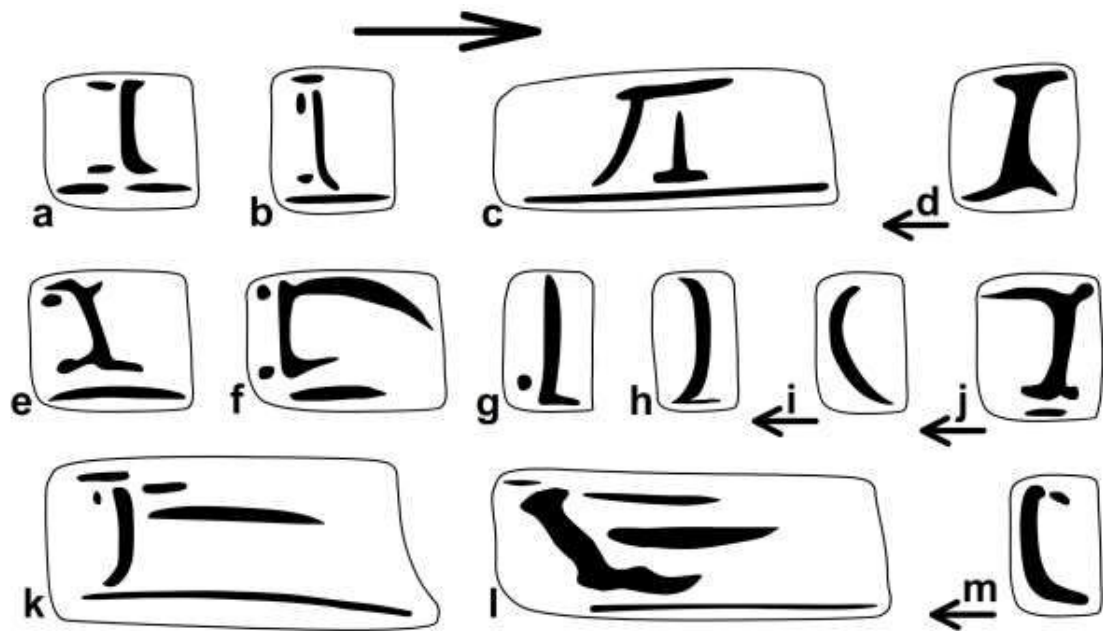


Figure 7.41. Parietal plicae and lamellae of *Endothyrella* species. a: *E. affinis*; b: *E. blanda*; c: *E. aborensis*; d: *E. munipurensis*; e: *E. pinacis*; f: *E. plectostoma*; g: *E. sowerbyi*; h: *E. bedfordi*; i: *E. babbagei*; j: *E. serica*; k: *E. williamsoni*; l: *E. brahma*; m: *E. oglei*. The arrow shows the direction of the aperture in sinistral species. Four drawings (d, i, j and m) show dextral species. In these cases the arrow under the latter indicates the direction on coiling.

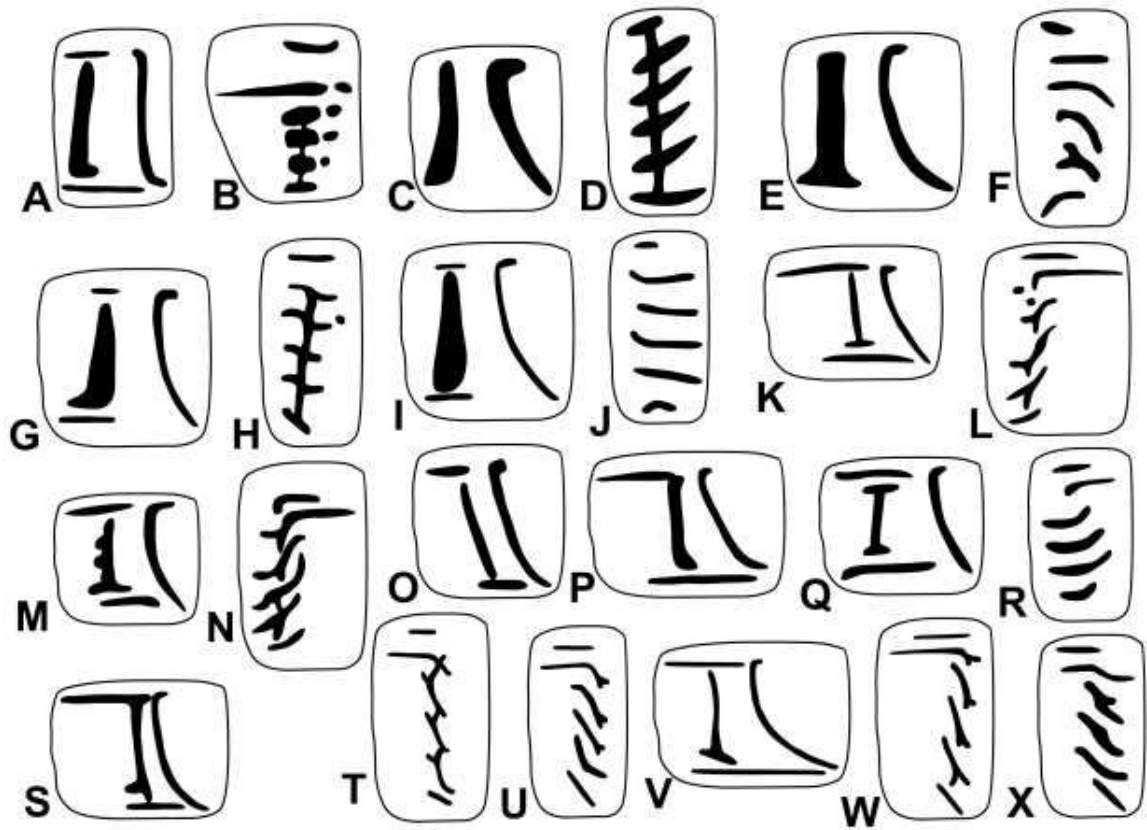


Figure 7.42. Parietal (A, C, E, G, I, K, M, O–Q, S) and palatal (B, D, F, H, J, L, N, R, T–U, W–X) plicae and lamellae of *Sicradiscus* and *Gudeodiscus* species. A–B: *Sicradiscus mansuyi* (Gude 1908), 20081116C (two different specimens); C–F: *Gudeodiscus (Gudeodiscus) anceyi* (Gude 1901), C–D: figures in Gude (1901a), E: MNHN-IM-2012-2263, F: GS22; G–J: *G. (G.) hemmeni* Páll-Gergely & Hunyadi u. sp., G–H: 2012/62, specimen1, I–J: 2012/62, specimen2; K–P: *G. (G.) phlyarius* (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*", 2 different specimens), X: Vn11-187. Inner view: D, L, N, R; Outer view: B, F, H, J, T, U, W, X.

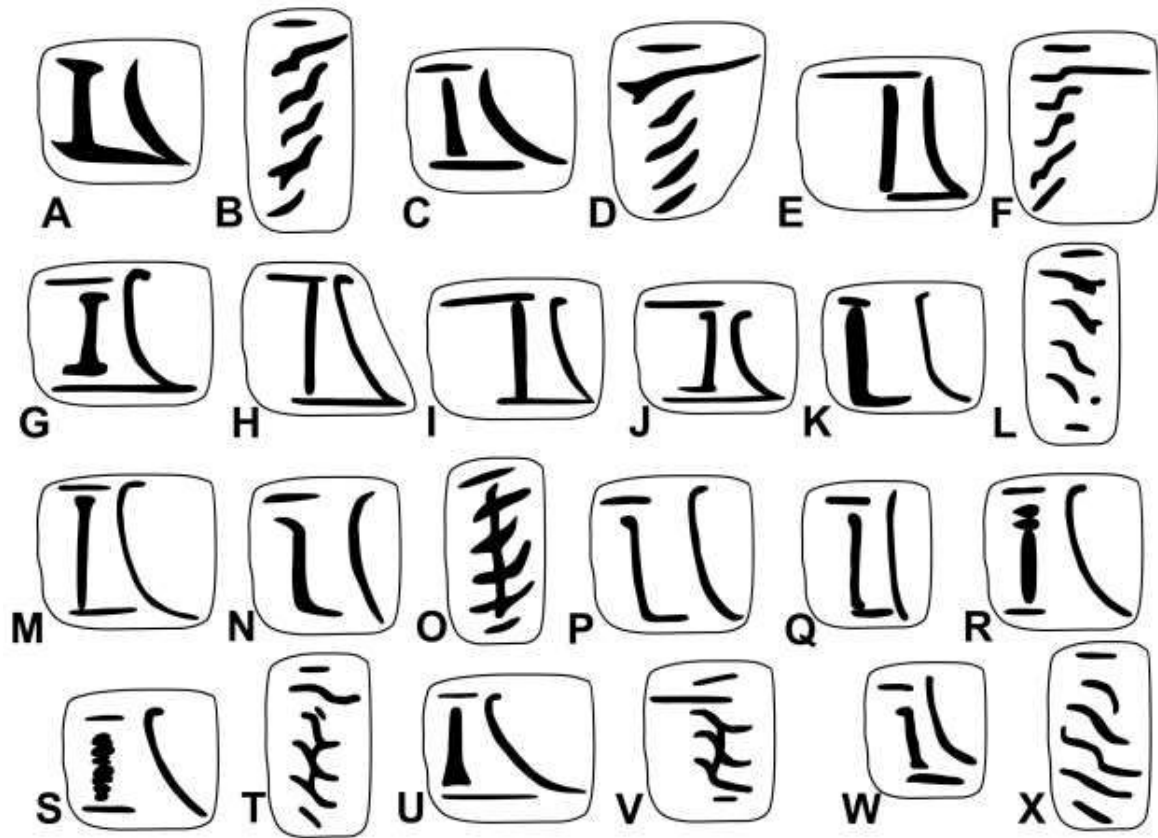


Figure 7.43. Parietal (A, C, E, G–K, M, N, P–S, U, W) and palatal (B, D, F, L, P, T, V, X) plicae and lamellae of *Gudeodiscus* species. A–M: *Gudeodiscus (Gudeodiscus) phlyarius* (Mabille 1887), A–B: *Plectopylis phlyaria* after Gude (1901c), C–D: *Plectopylis moellendorffi* after Gude (1901c), E–F: 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.) messengeri messengeri* (Gude 1909), N–O: *Plectopylis messengeri* (after Gude 1909), P: MNHN-IM-2012-2162, Q: MNHN-IM-2012-2165; R–V: *G. (G.) messengeri raheemi* u. ssp., 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.

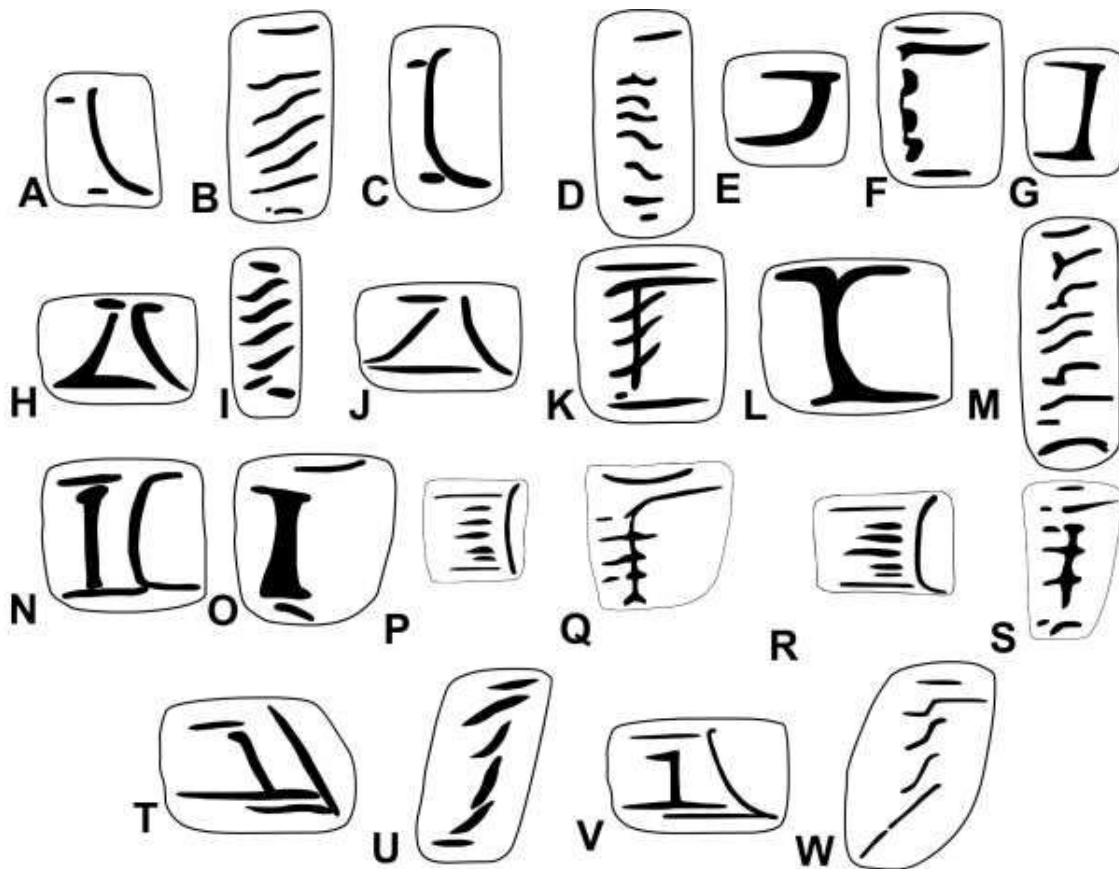


Figure 7.44. Parietal (A, C, E, G, H, J, L, N, P, R, T, V) and palatal (B, D, F, I, K, M, O, Q, S, U, W) plicae and lamellae of *Gudeodiscus* species. A–B: *Gudeodiscus pulvinaris robustus* Páll-Gergely & Hunyadi 2013, paratype from the type locality; C–D: *Gudeodiscus concavus* Páll-Gergely 2013, paratype from the type locality; 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–M: *Gudeodiscus goliath* Páll-Gergely & Hunyadi 2013, paratype from the type locality; N–O: *Gudeodiscus yanghaoi* Páll-Gergely & Hunyadi 2013, paratype from the type locality; P–S: *Gudeodiscus ursula* Páll-Gergely & Hunyadi 2013, paratypes from the type sample; T–W: *G. (G.) villedaryi* (Ancey 1888), T–U: holotype of *Plectopylis (Endoplona) choanomphala* Möllendorff 1901 (after Gude 1901c), V–W: Vn10-47A. Inner views: B, F, I, K, M, Q, S, U, W; Outer views: D, O.

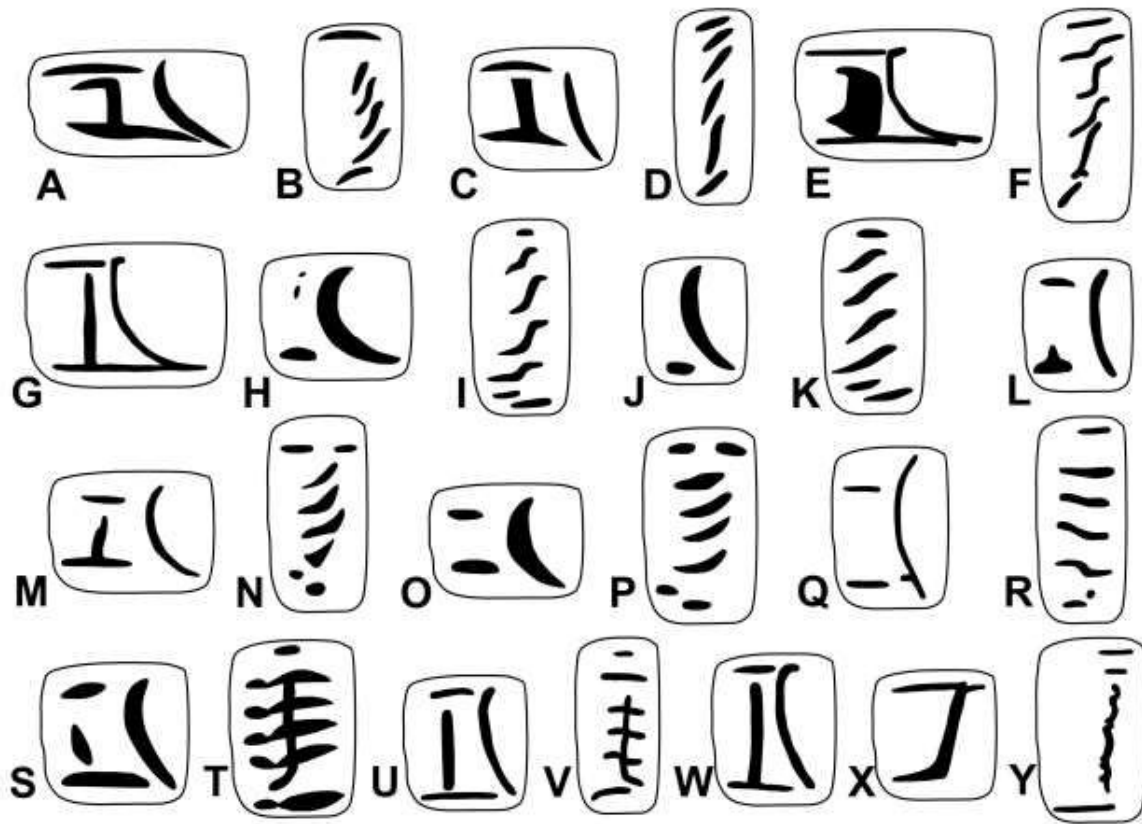


Figure 7.45. Parietal (A, C, E, G, H, J, L, M, O, Q, S, U, W, X) and palatal (B, D, F, I, K, N, P, R, T, V, Y) plicae and lamellae of *Gudeodiscus* and *Halongella* u. gen. species. A–G: *Gudeodiscus* (*Gudeodiscus*) *dautzenbergi* (Gude 1901), A–B: *G. (G.) dautzenbergi* (Gude 1901) (after Gude 1901a), 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.

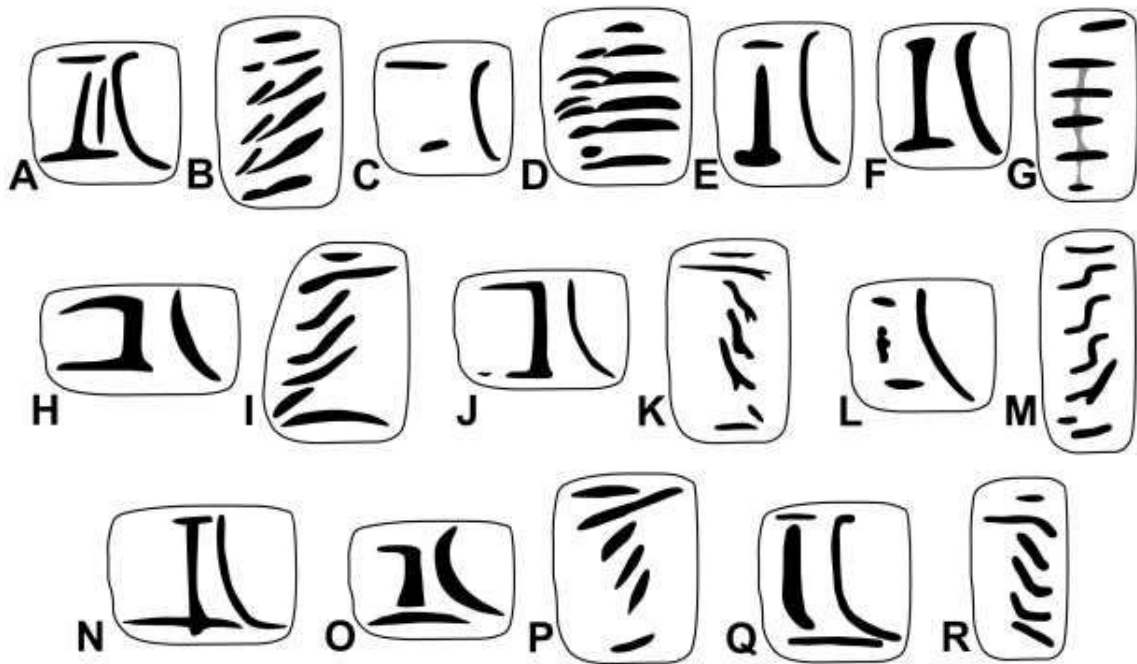


Figure 7.46. Parietal (A, C, E, F, H, J, L, N, O, Q) and palatal (B, D, G, I, K, M, P, R) plicae and lamellae of *Gudeodiscus* species. A–D: *Gudeodiscus (Gudeodiscus) infralevi*s (Gude 1908), A–B: holotype of "*Plectopylis infralevi*s" after Gude (1908), C–D: "*Plectopylis soror*" after Gude (1908); 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.

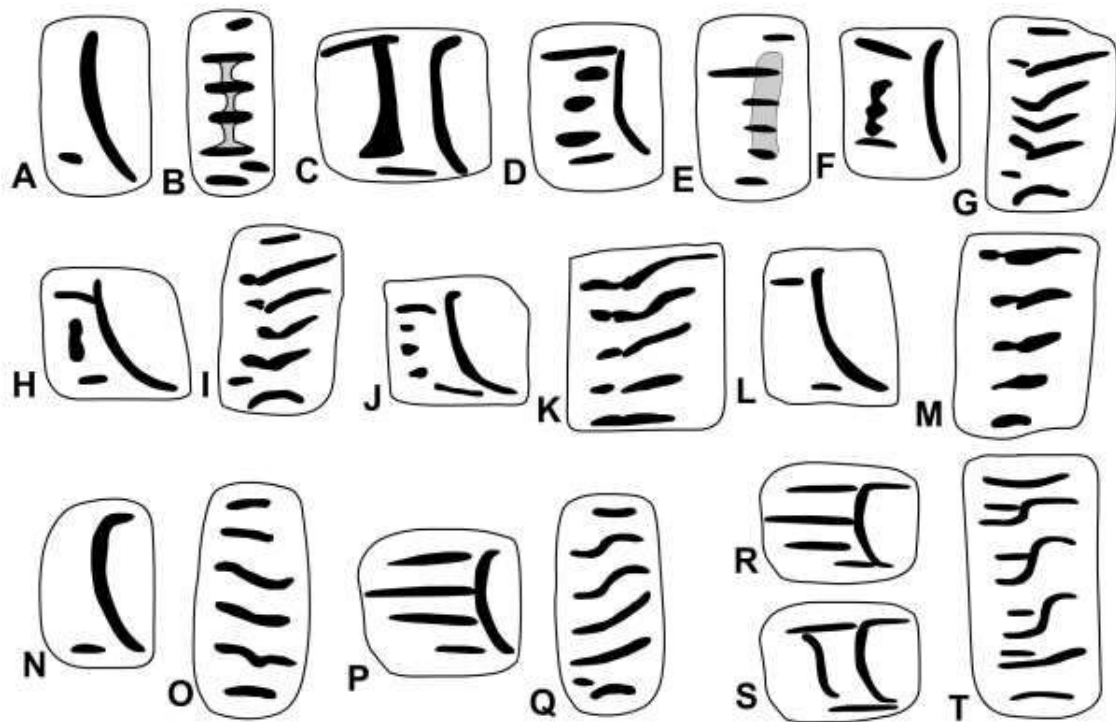


Figure 7.47. Parietal (A, C, D, F, H, J, L, N, P, R, S) and palatal (B, E, G, I, K, M, O, Q, T) lamellation of *Gudeodiscus* species. A–B: *Gudeodiscus yunnanensis* Páll-Gergely 2013, paratype from the type locality; C: *Gudeodiscus cyrtochilus* (Gude 1909), specimen from Kong Shancun; textfigs. D–E: *Gudeodiscus soosi* Páll-Gergely 2013, paratype from the type locality; F–M: *Gudeodiscus multispira* (Möllendorff 1883), F–I: population from Lipu, J–K: population from the Lotus Cave, L–M: population from Diecaishan; N–O: *Gudeodiscus emigrans emigrans* (Möllendorff 1901) holotype; P–Q: *Gudeodiscus emigrans quadrilamellatus* Páll-Gergely 2013, paratype from the type locality; R–T: *Gudeodiscus emigrans otanii* Páll-Gergely 2013, R: paratype from the type locality; S–T: holotype. Inner views: G, I, K, M, Q, T, outer views: B, E, O.

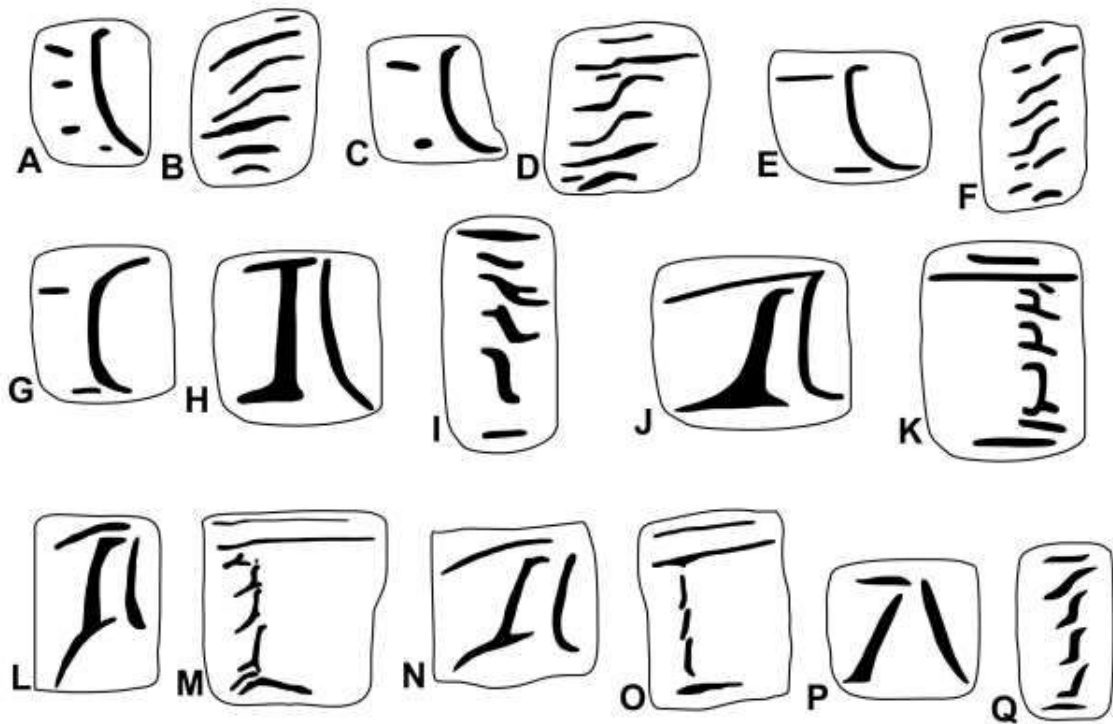


Figure 7.48. Parietal (A, C, E, G, H, J, L, N, P) and palatal (B, D, F, I, K, M, O, Q) lamellation of *Gudeodiscus* species. A–D: *Gudeodiscus eroessi* Páll-Gergely & Hunyadi 2013, paratypes from Chuan Shancun; E–F: *Gudeodiscus okuboi* Páll-Gergely & Hunyadi 2013, paratype from the type locality; G: *Gudeodiscus eroessi fuscus* Páll-Gergely & Hunyadi 2013, paratype; H–I: *Gudeodiscus giardi* (Fischer 1898), specimen from Shuikou town; J–K: *Gudeodiscus giardi oharai* Páll-Gergely 2013, paratype from the type locality; L–O: *Gudeodiscus giardi szekeresi* Páll-Gergely & Hunyadi 2013, paratype from the type locality; P: *Plectopylis giardi* (after Gude 1899b), Q: *Plectopylis giardi* (after Gude 1899d). Inner views: B, D, F, M, O, Q; outer views: I, K.

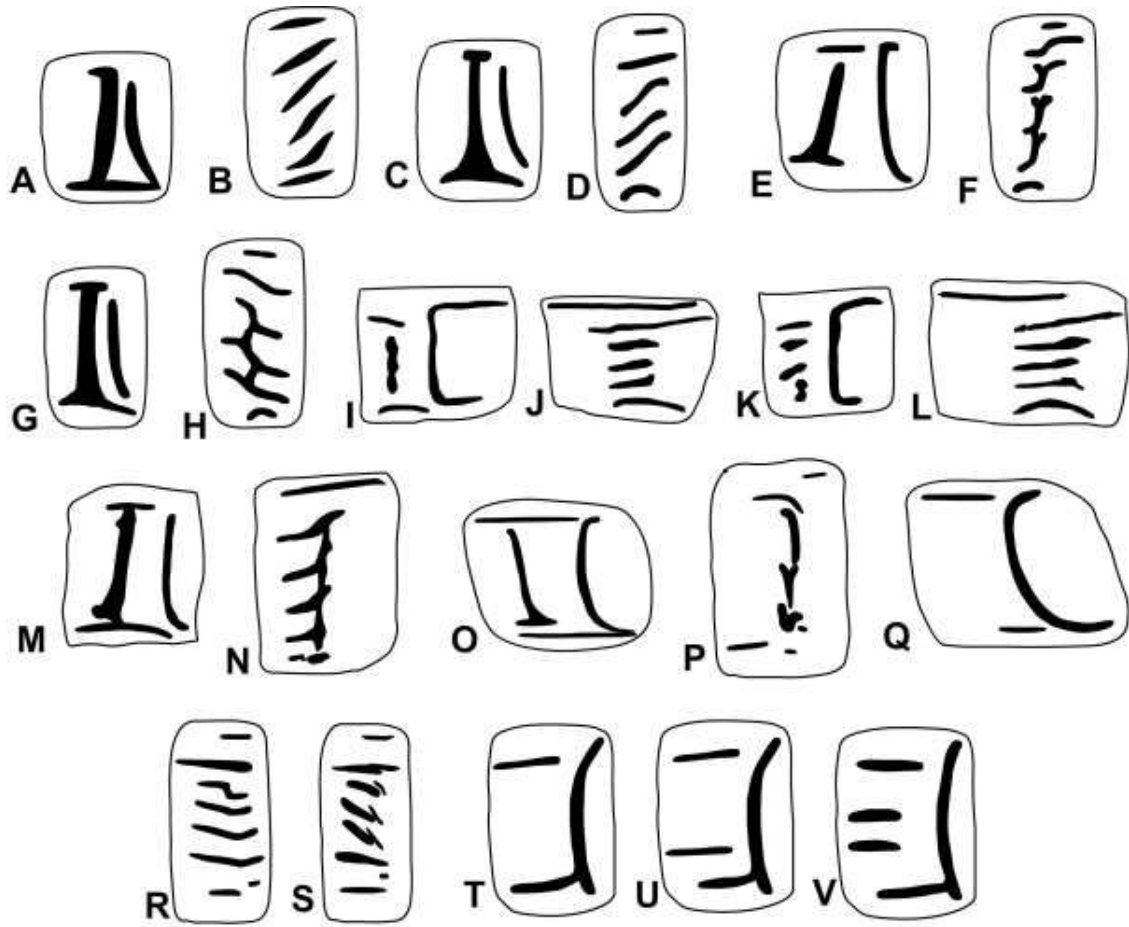


Figure 7.49. Parietal (A, C, E, G, I, K, M, O, Q, T–V) and palatal (B, D, F, H, J, L, N, P, R, S) lamellation of *Gudeodiscus* and *Sinicola* species. A–H: *G. (G.) giardi giardi* (Fischer 1898), A–B: *Plectopylis congesta* Gude 1899 (after Gude 1899b); C–D: Vn10-69, E–F: Vn10-59, G–H: 2011/85; I–L: *Gudeodiscus phlyarius* (Mabille 1887), (paratypes of *wernerii* Páll-Gergely 2013 from the type locality); M–N: *Gudeodiscus phlyarius*, specimen from the Peri Hill; O–P: *Gudeodiscus marmoreus* Páll-Gergely 2014 (holotype); Q: *Sinicola vargabalinti* Páll-Gergely 2014, HHNM 97455, holotype; R: *S. vargabalinti*, HHNM 97456, paratype; S: *S. vargabalinti*, HHNM 97455, holotype; T–V: *Sinicola schmackeri* Páll-Gergely 2013, paratypes from the type sample. Inner views: B, D, F, J, L, N; outer view: H, P, R, S.

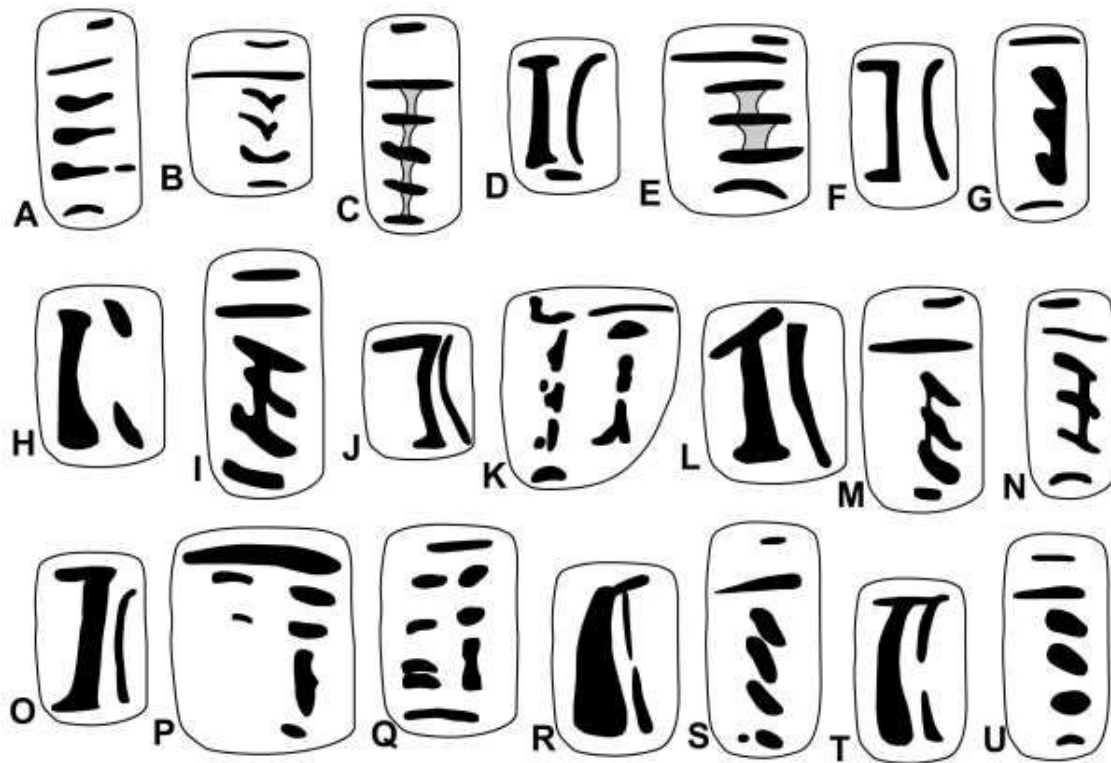


Figure 7.50. Parietal (D, F, H, J, L, O, R, T) and palatal (A, B, C, E, G, I, K, M, N, P, Q, S, U) lamellation of *Sicradiscus* and *Sinicola* species. A–B: *Sinicola stenochila* (Möllendorff 1885), specimen from Huayan Dong; B: *Sinicola biforis* (Heude 1885), paratype; C: *Sinicola murata* (Heude 1885), specimen from Tiantaishan; D–E: *Sicradiscus feheri* Páll-Gergely & Hunyadi, 2013, paratype from the type locality; F–G: *Sicradiscus invius* (Heude 1885), 20070708B; H–I: *Sicradiscus cutisculpta* (Möllendorff 1882), NHMW 40168; J–K: *Sicradiscus schistoptychia* (Möllendorff 1886), 2010/48; L–M: *Sicradiscus diptychia* (Möllendorff 1885), specimen from Jinji Dong; N: *Sicradiscus securus* (Heude 1889), lectotype MCZ 167129; O–Q: *Sicradiscus transitus* Páll-Gergely 2013, paratype from the type locality; R–S: *Sicradiscus ishizakii* (Kuroda 1941), Taiwan, BaLing, Tao Yuang Xian, leg. Okubo, K; T–U: *Sicradiscus hirasei* (Pilsbry 1904), Mt. Nobaru, Miyako Island, Okinawa, Japan, leg. Minato. All figures from outer views.

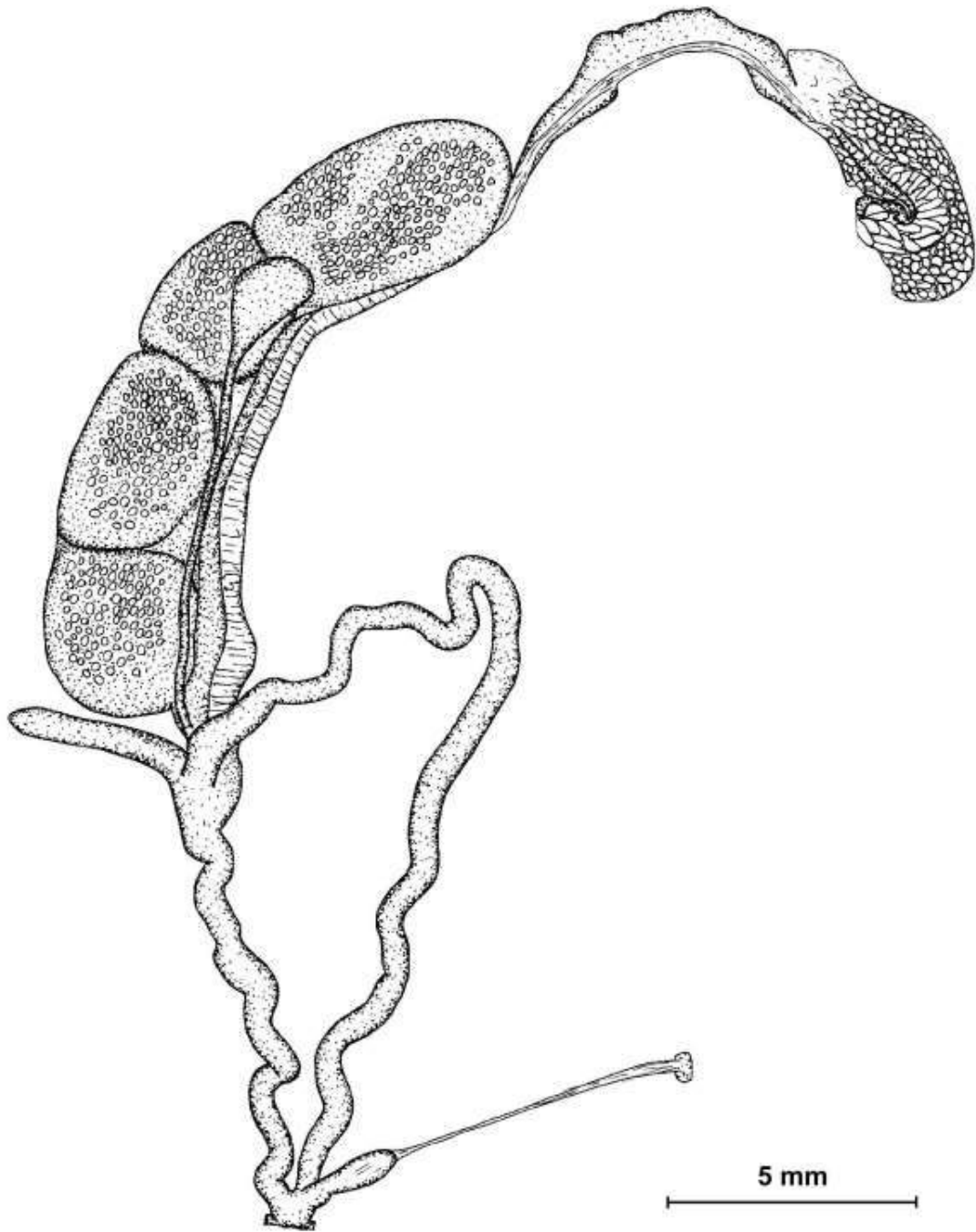


Figure 7.51. *Genus1 dextrorsa* (Benson 1860)

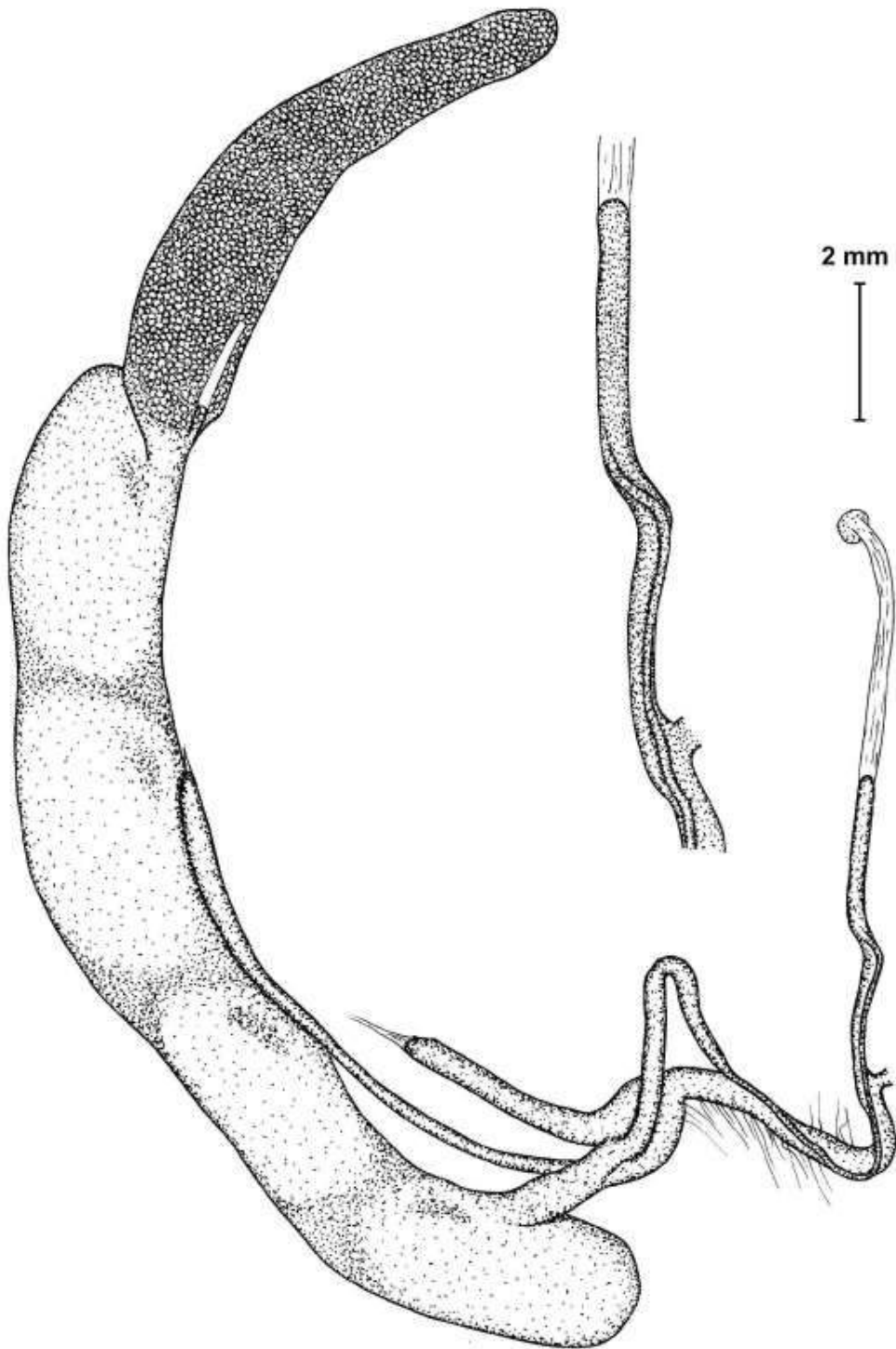


Figure 7.52: *Chersaecia perrieri* (Gude 1897)

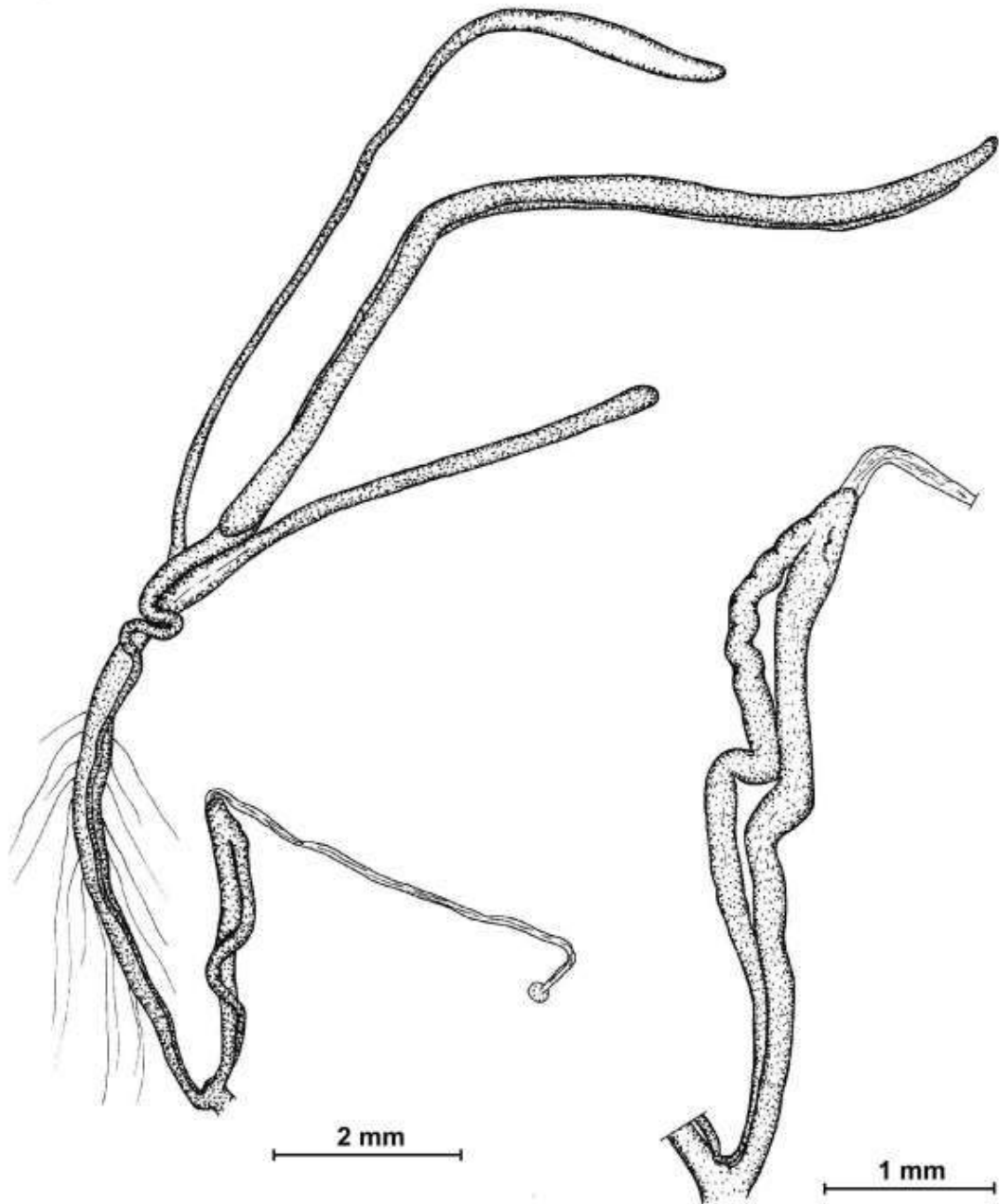


Figure 7.53: *Chersaecia shanensis* (Stoliczka 1873)

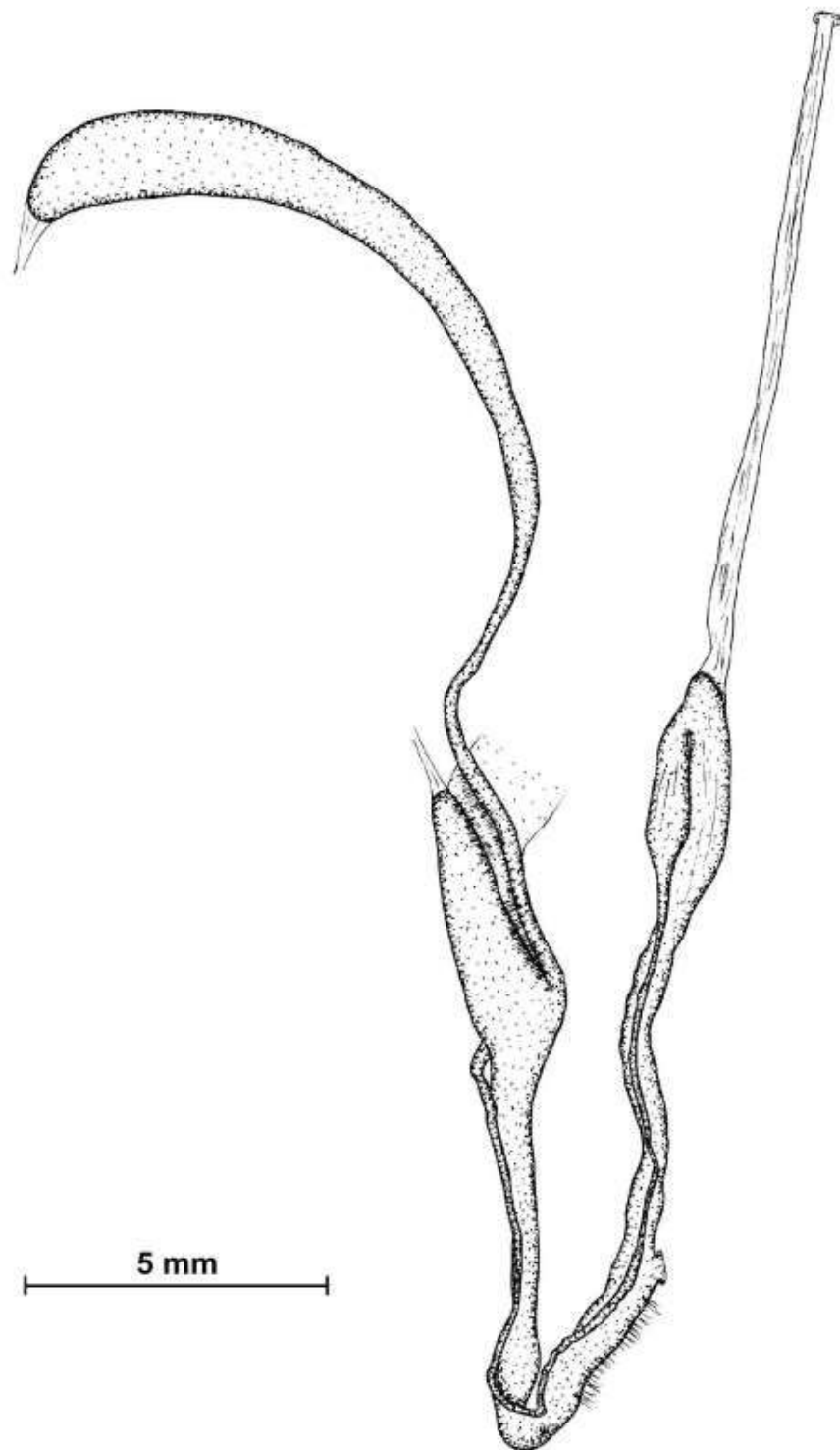


Figure 7.54: *Plectopylis bensoni* Gude 1914

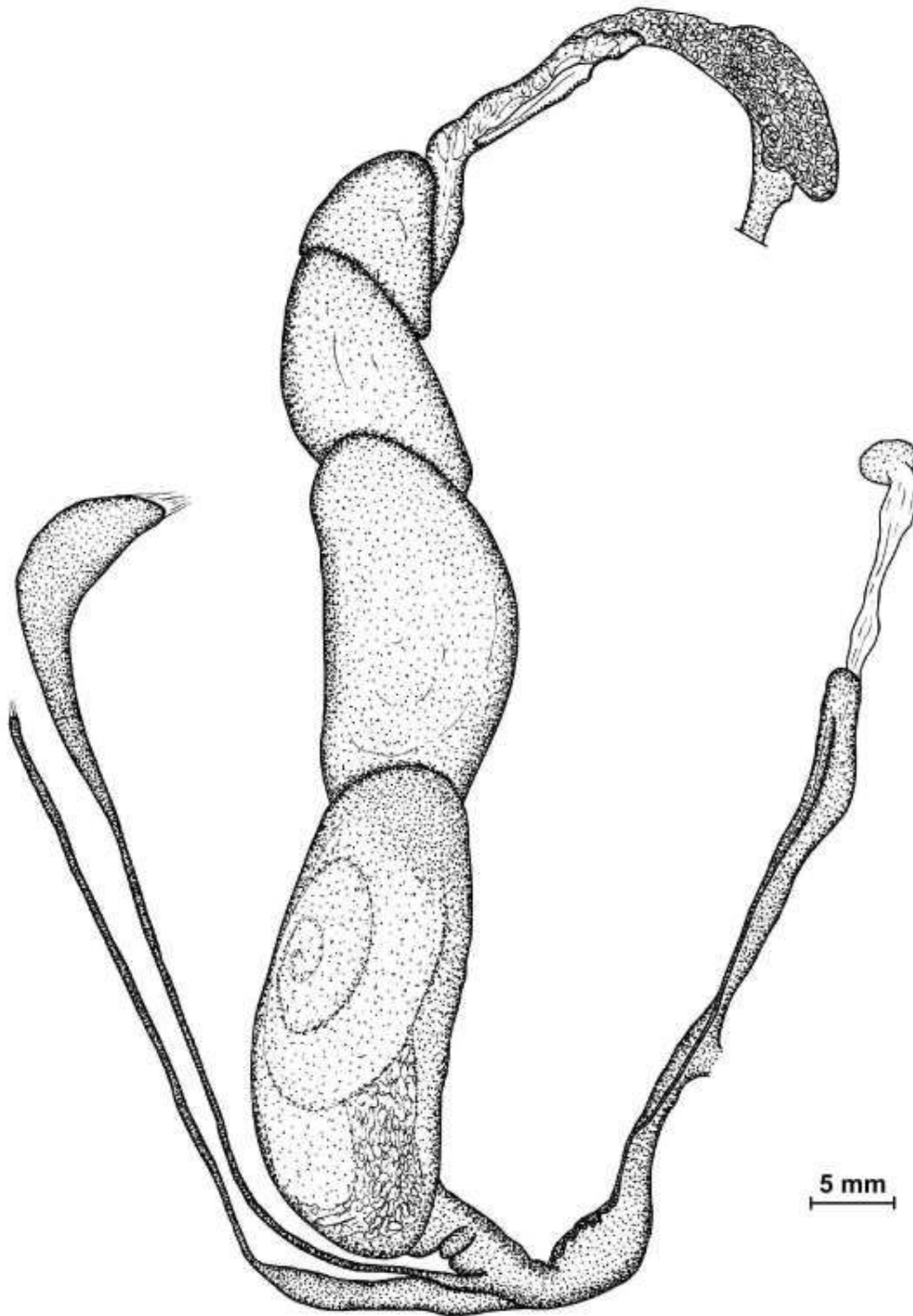


Figure 7.55: *Plectopylis* species2 u. sp.

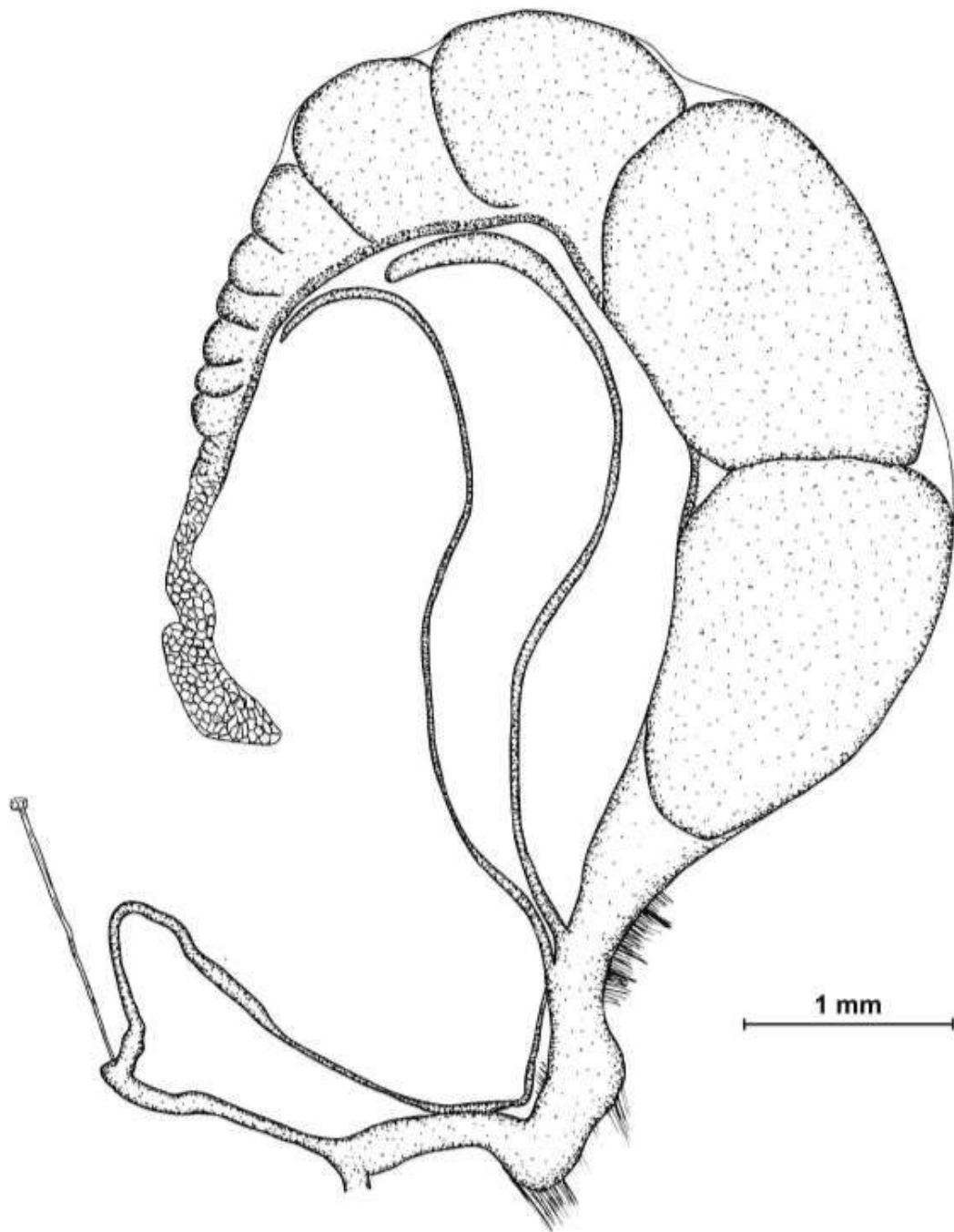


Figure 7.56: *Endothyrella blanda* (Gude 1897)

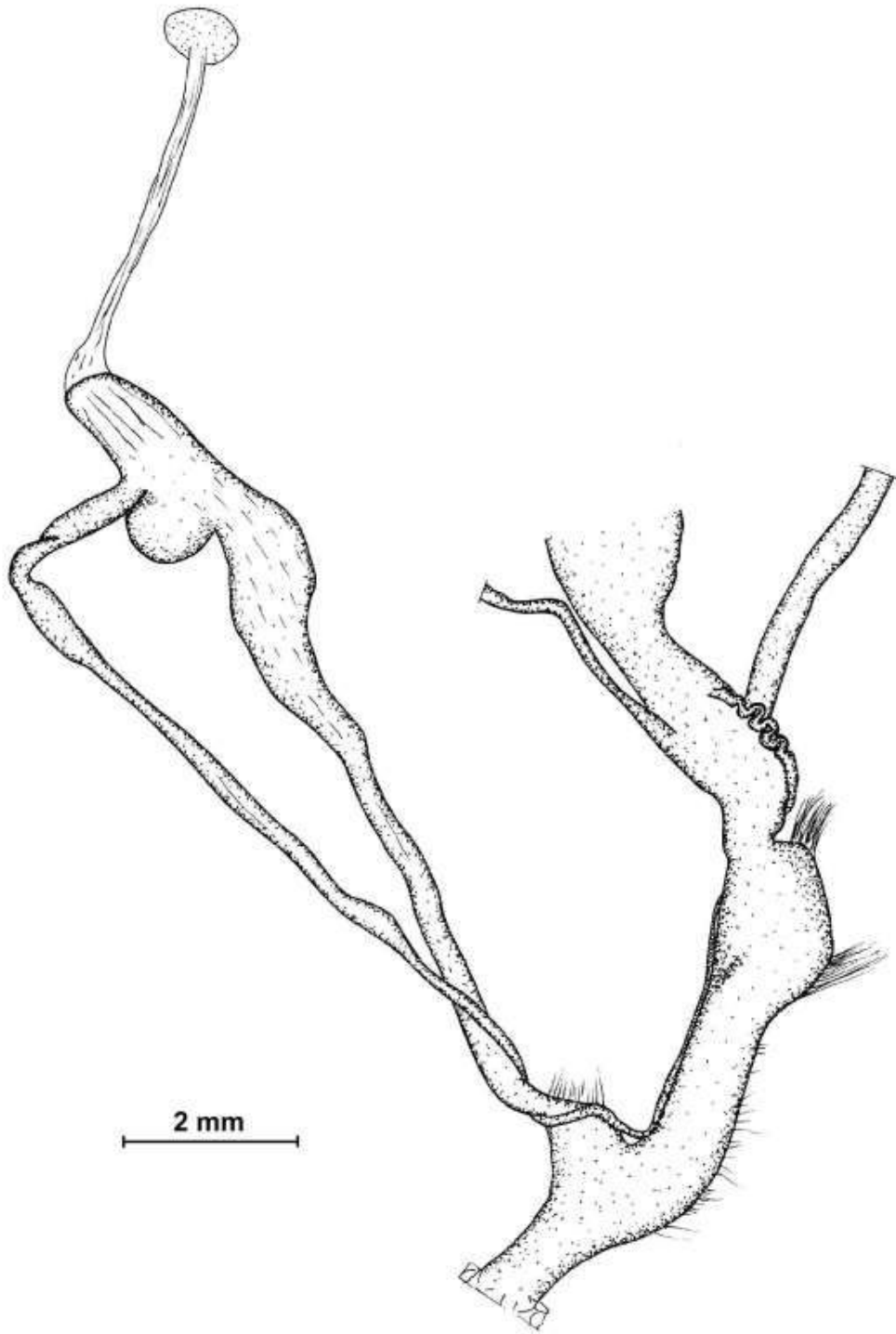


Figure 7.57: *Endothyrella fultoni* (Godwin-Austen 1892)

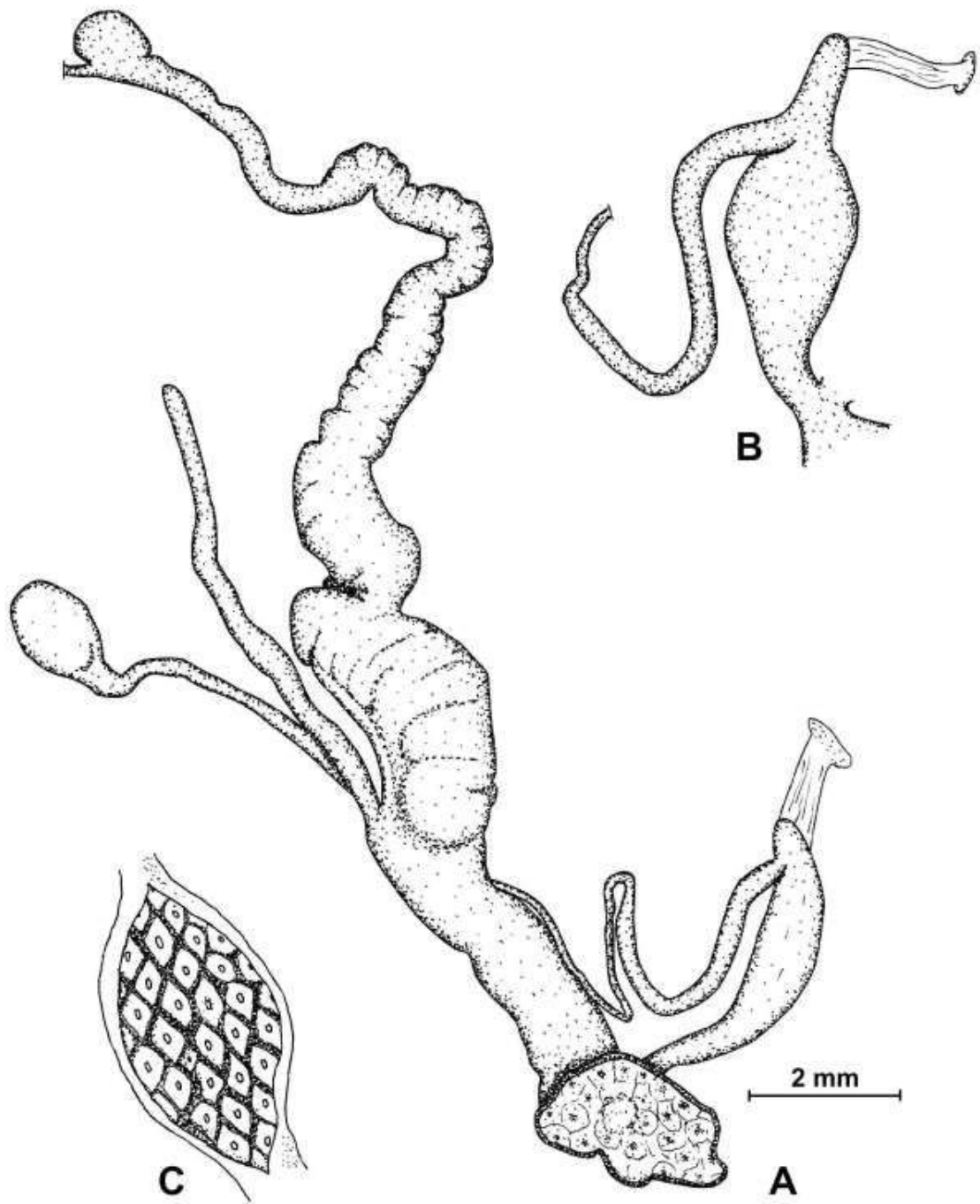


Figure 7.58: *Endothyrella* species8 u. sp.

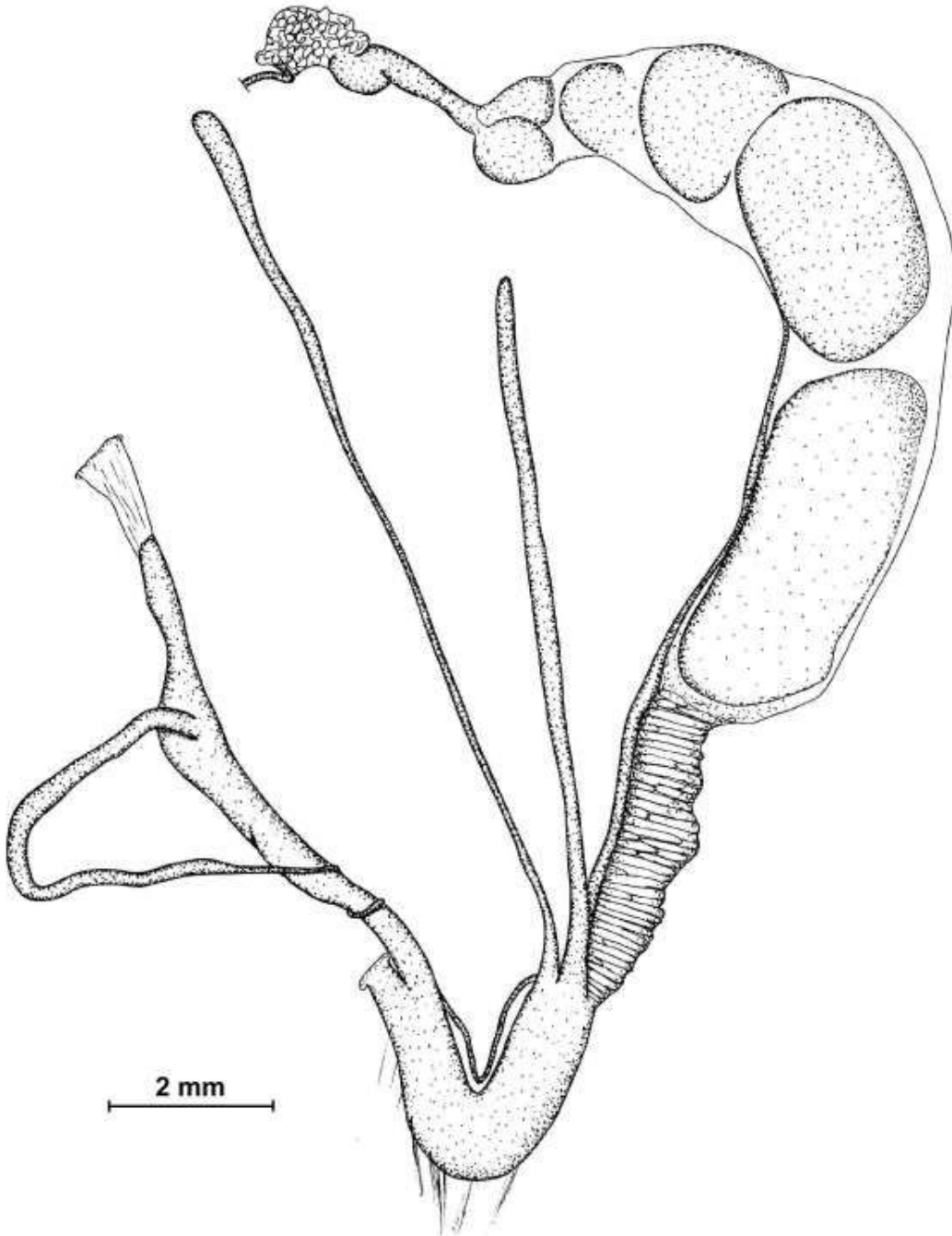


Figure 7.59: *Endothyrella plectostoma* (Benson 1836)

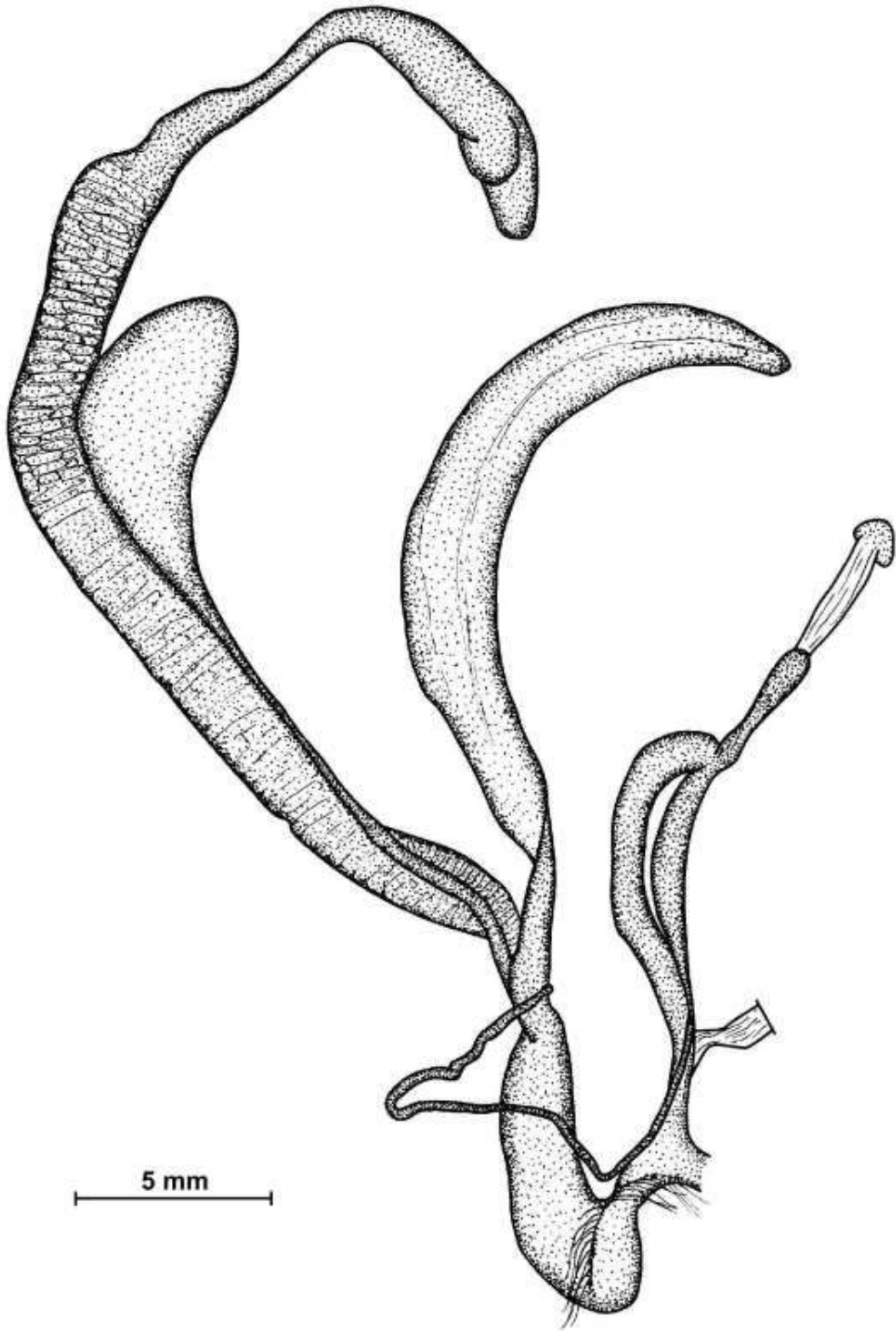


Figure 7.60: *Gudeodiscus (Gudeodiscus) fischeri* (Gude 1901) Vn11-138

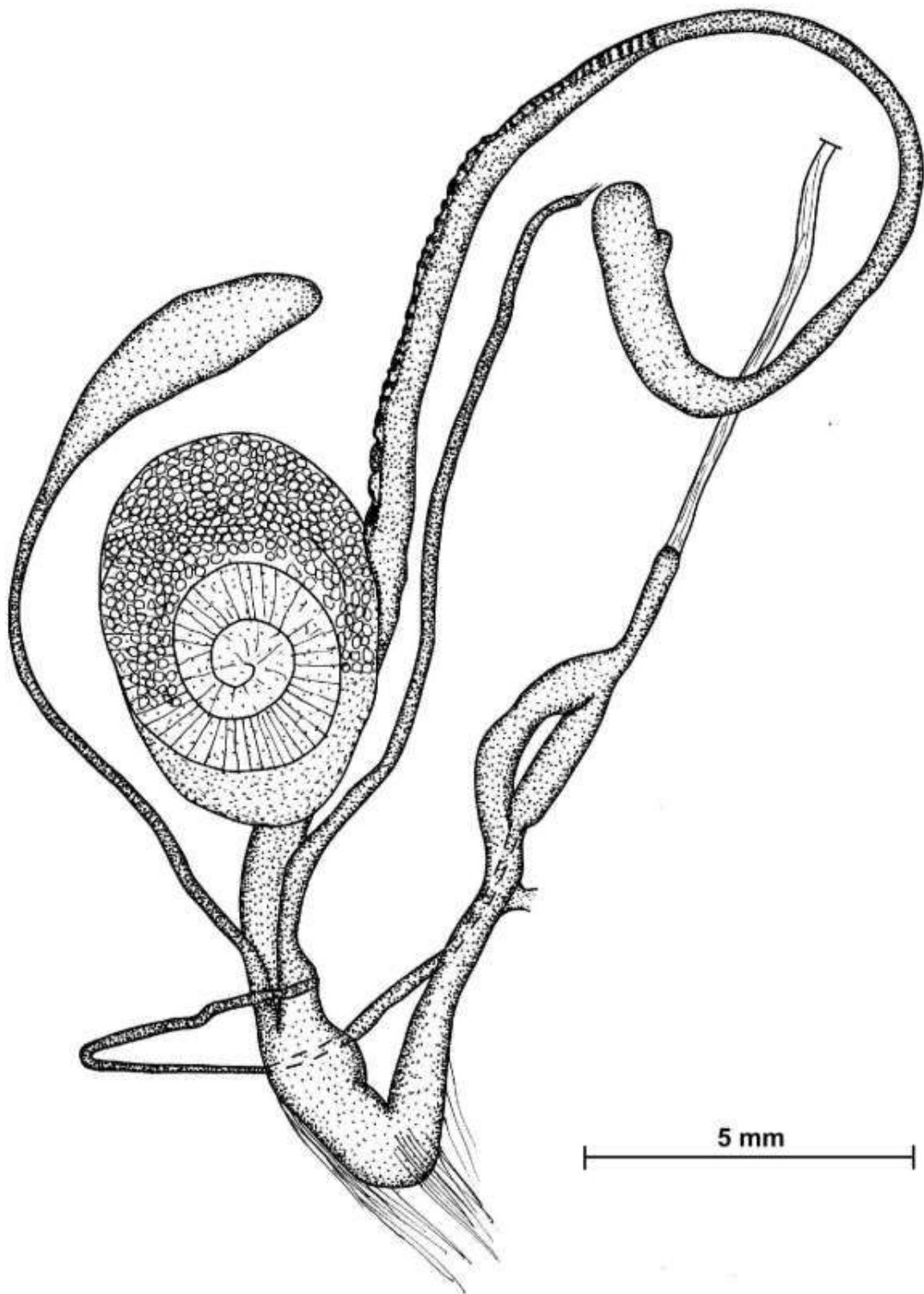


Figure 7.61: *Gudeodiscus (Gudeodiscus) fischeri* (Gude 1901) 2011.96

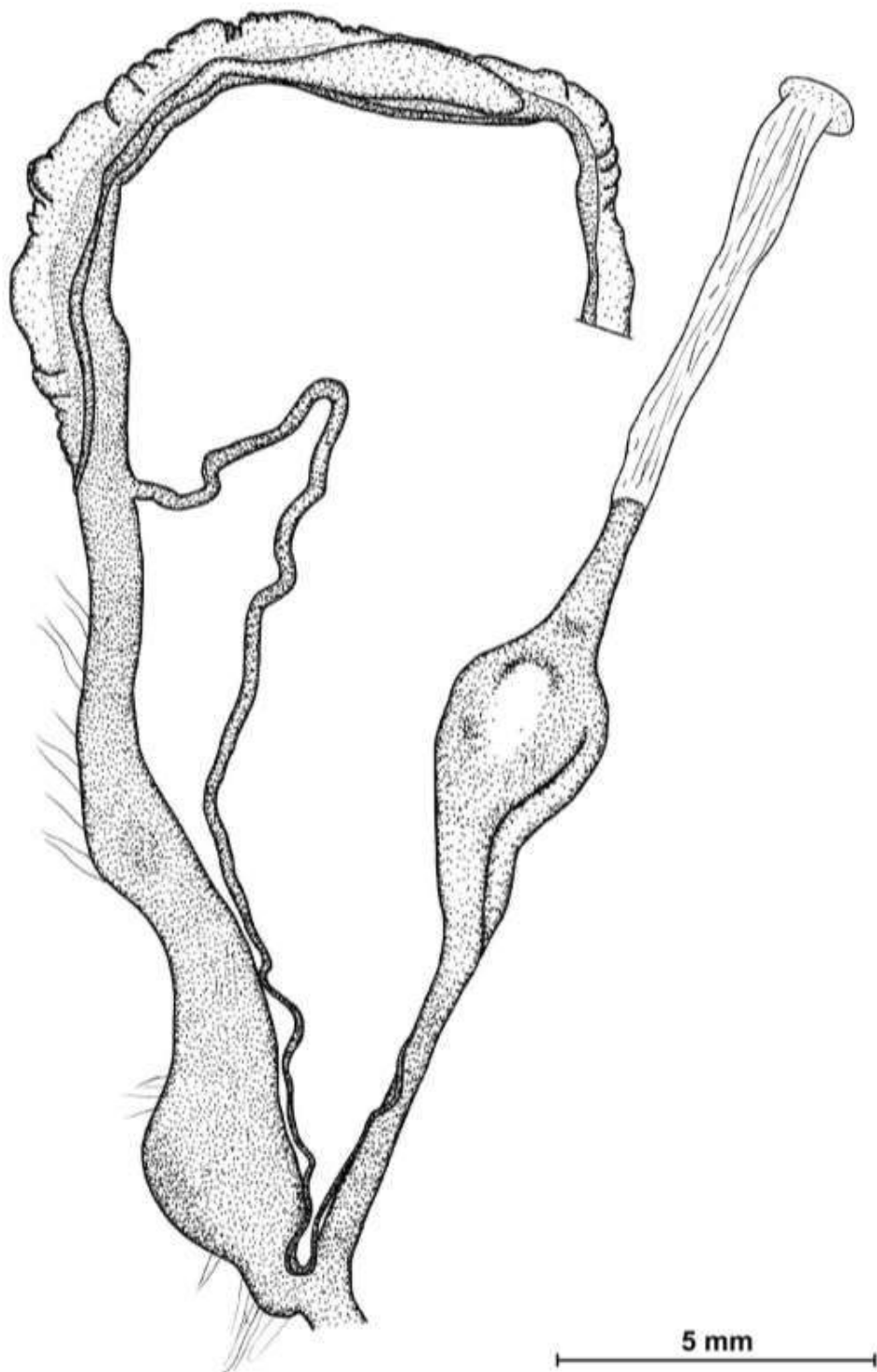


Figure 7.62: *Gudeodiscus (Gudeodiscus) giardi* (H. Fischer 1898) 2006.01.10E

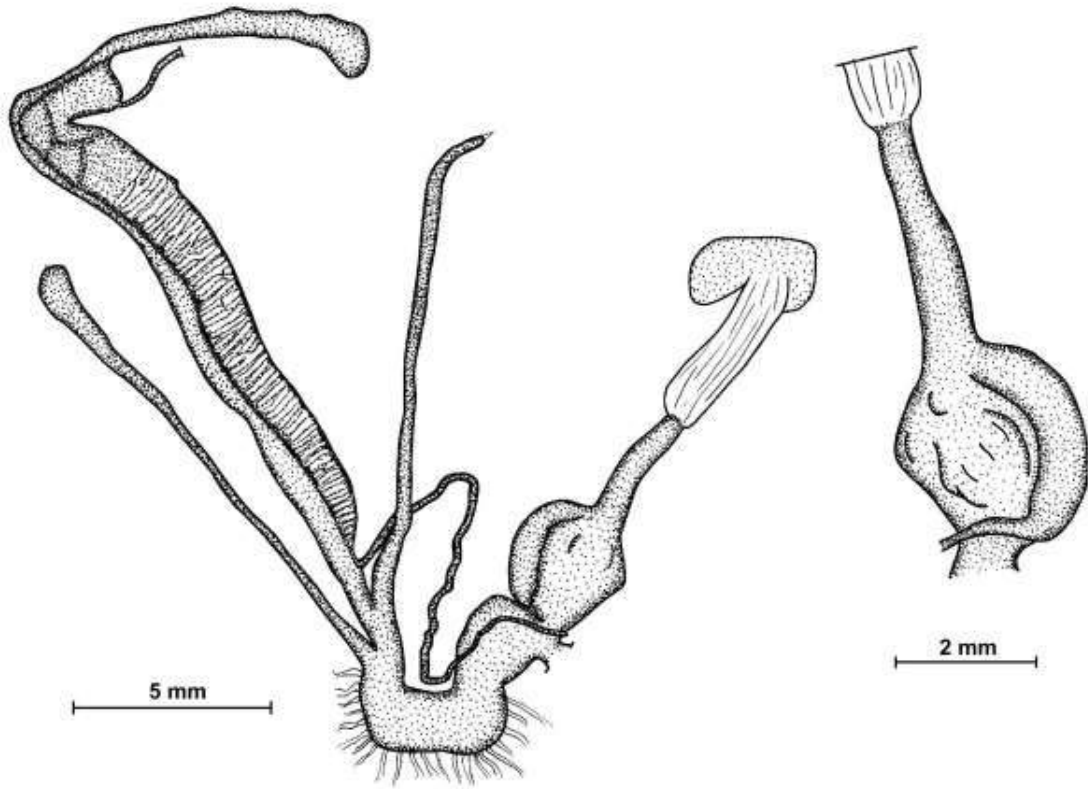


Figure 7.63: *Gudeodiscus (Gudeodiscus) giardi* (H. Fischer 1898) 2011/87

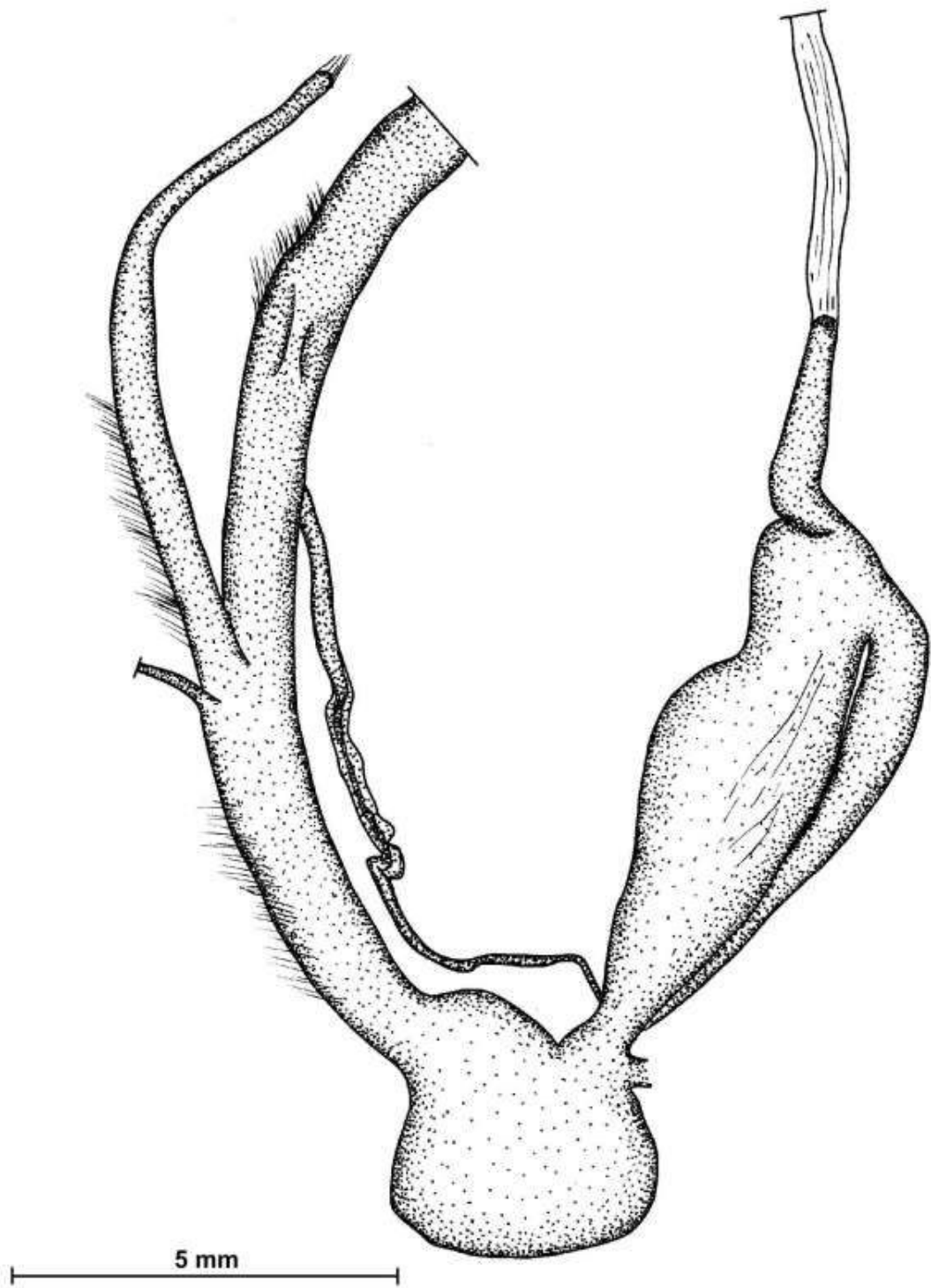


Figure 7.64: *Gudeodiscus (Gudeodiscus) messengeri raheemi* Páll-Gergely & Hunyadi u. ssp. Laos

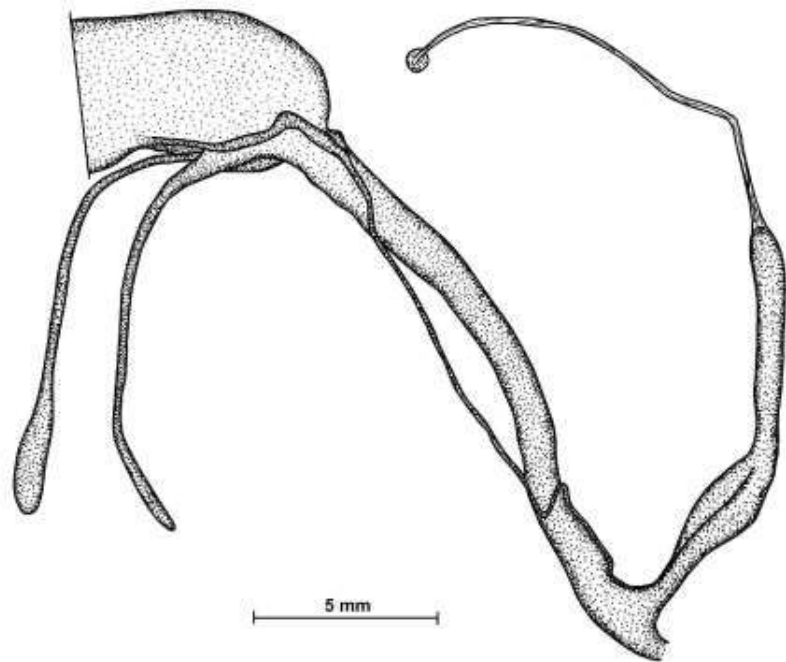


Figure 7.65: *Gudeodiscus (G.) messageri raheemi* Páll-Gergely & Hunyadi u. ssp. 2008.05.10A

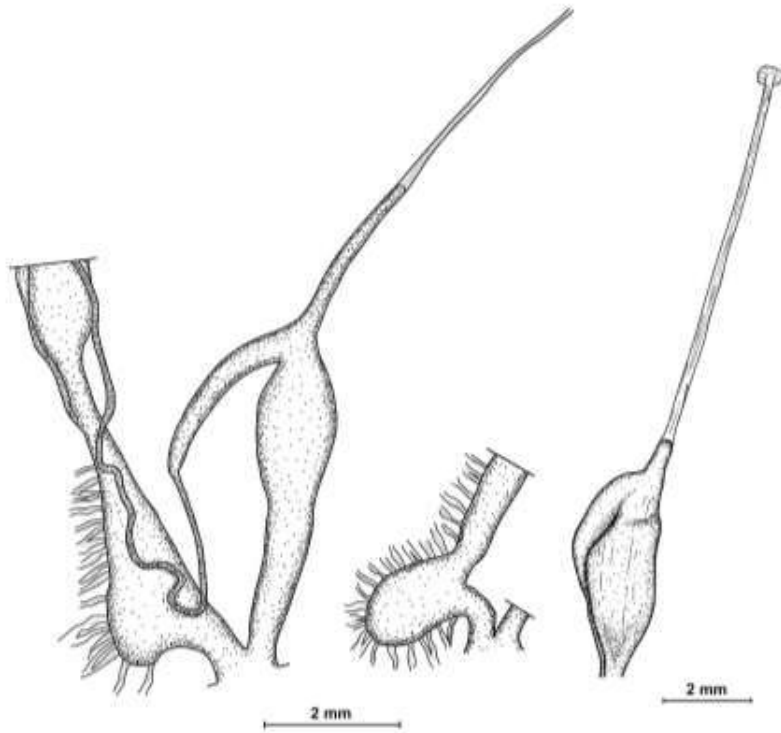


Figure 7.66: *Gudeodiscus (Gudeodiscus) multispira* (Möllendorff 1883)

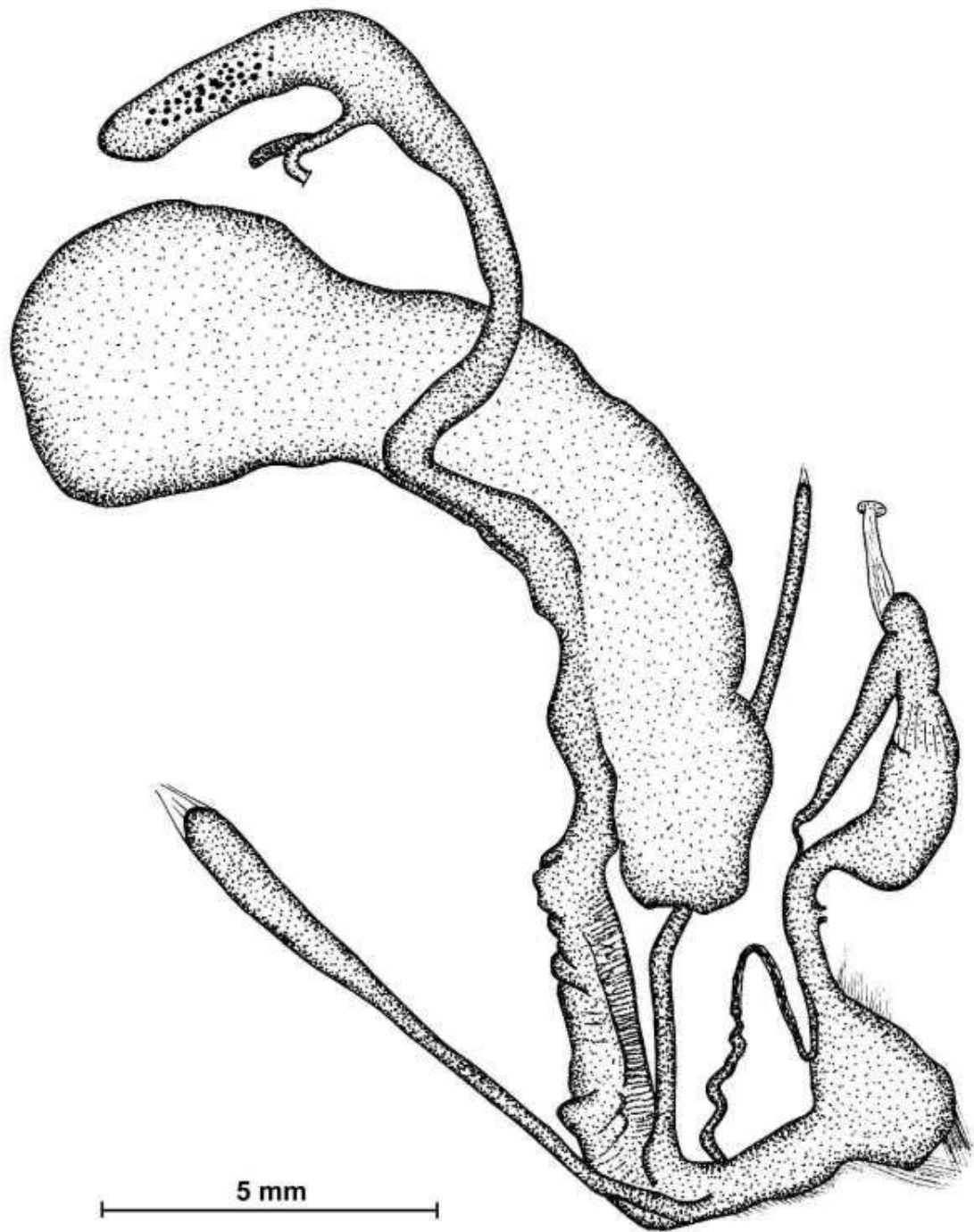


Figure 7.67: *Gudeodiscus (Gudeodiscus) phlyarius* (Mabille 1887) Vn11-156

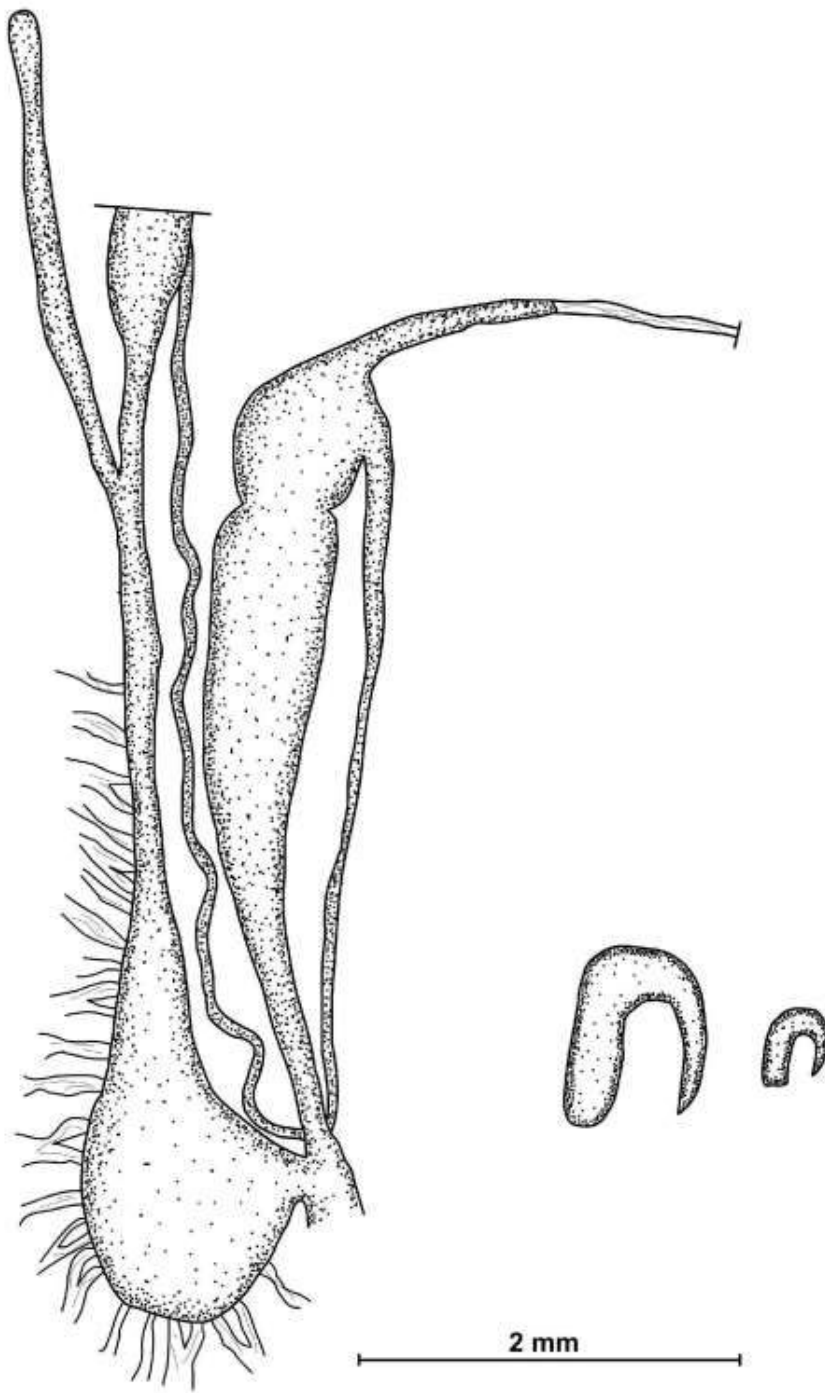


Figure 7.68: *Gudeodiscus (Gudeodiscus) phlyarius* (Mabille 1887) 2009/81.

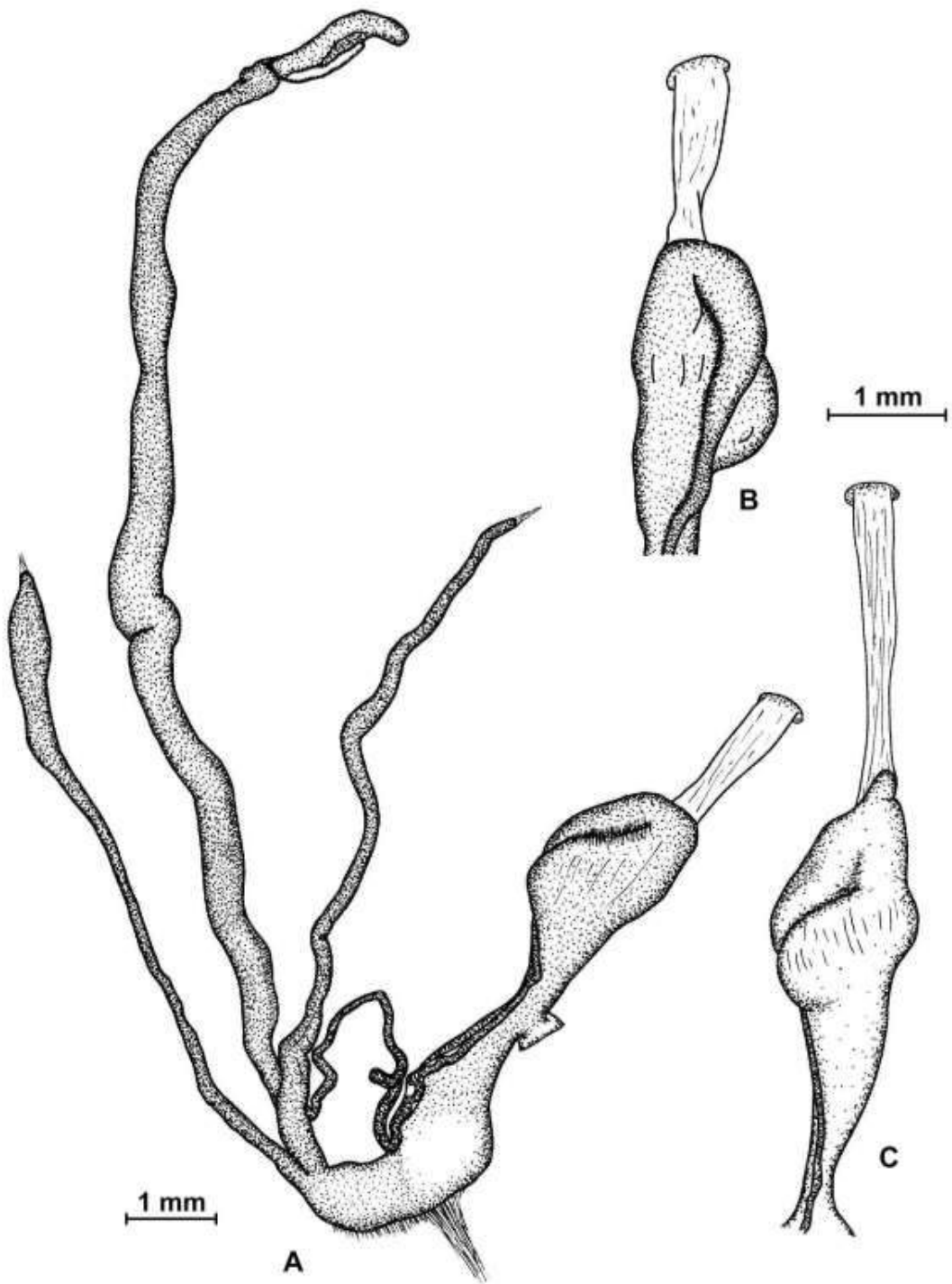


Figure 7.69: *Gudeodiscus (Gudeodiscus) phlyarius* (Mabille 1887) Vn11-187

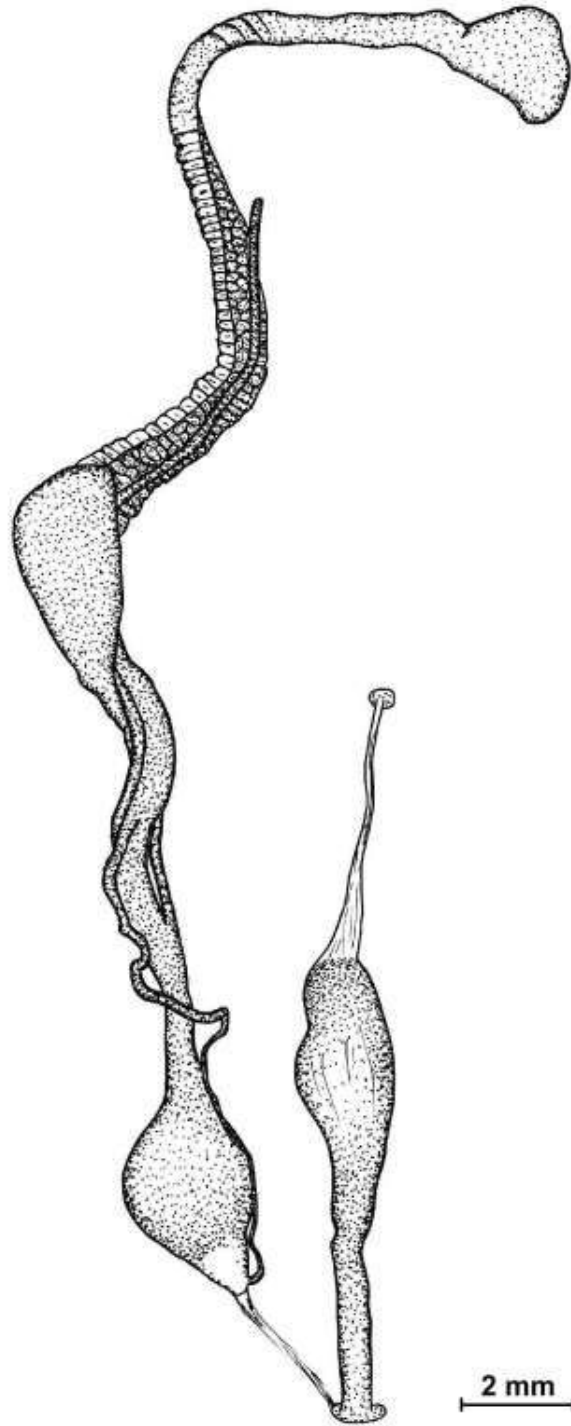


Figure 7.70: *Gudeodiscus* (*Gudeodiscus*) *villedaryi* (Ancey 1888)

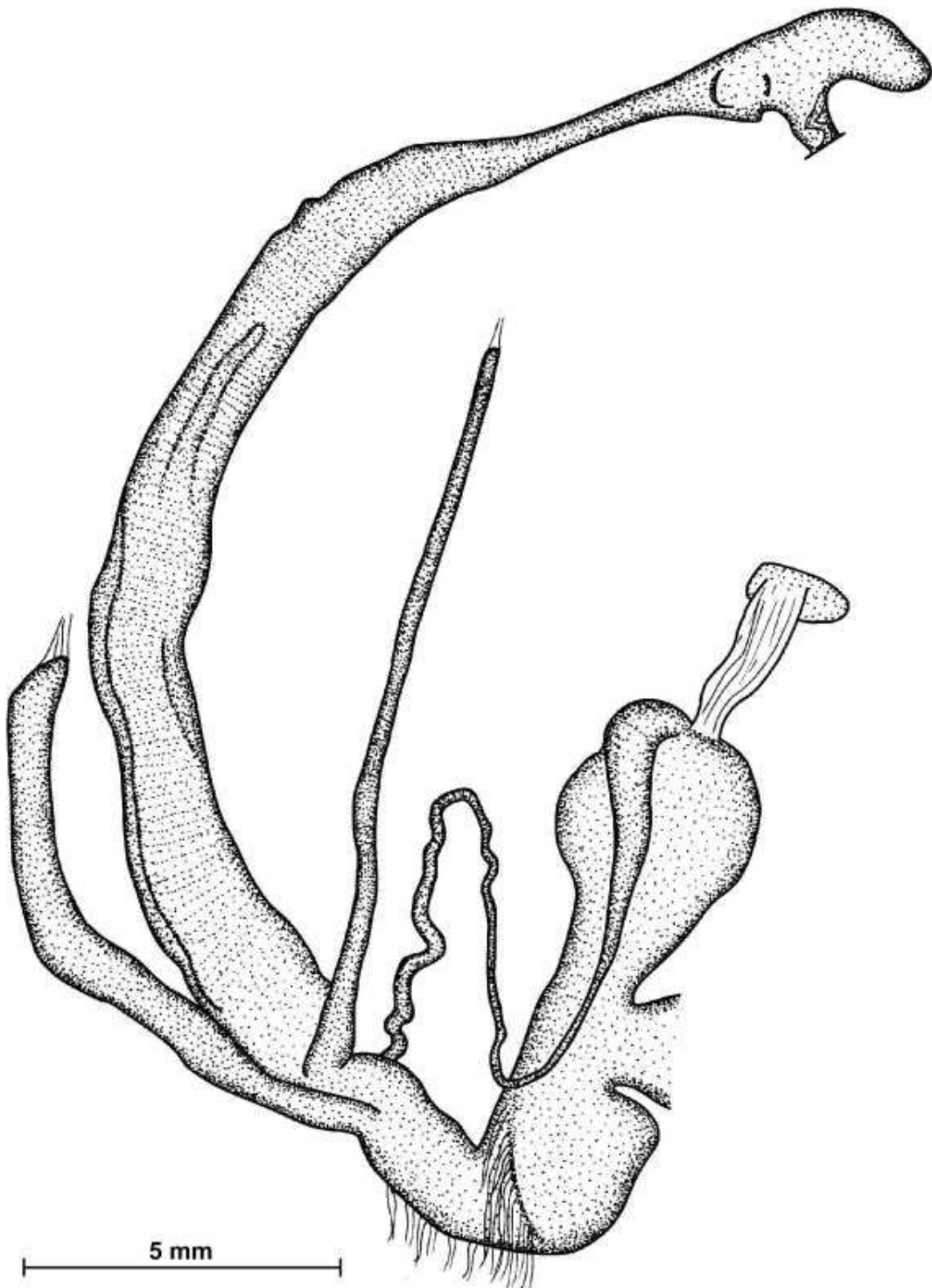


Figure 7.71: *Gudeodiscus (Gudeodiscus) villedaryi* (Ancey 1888)

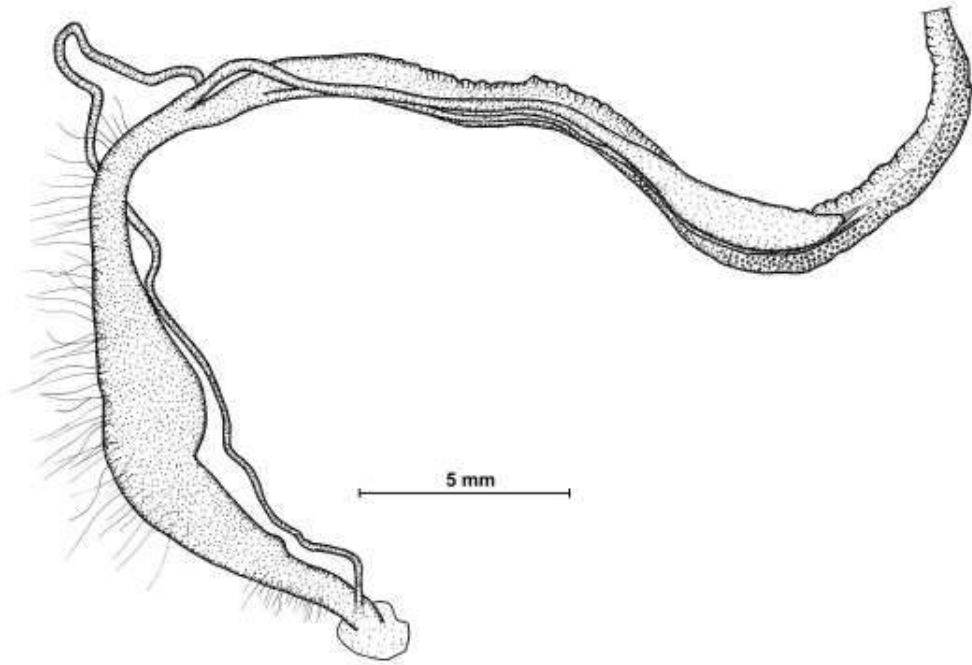


Figure 7.72: *Gudeodiscus (Veludiscus) emigrans otanii* Páll-Gergely & Hunyadi 2013

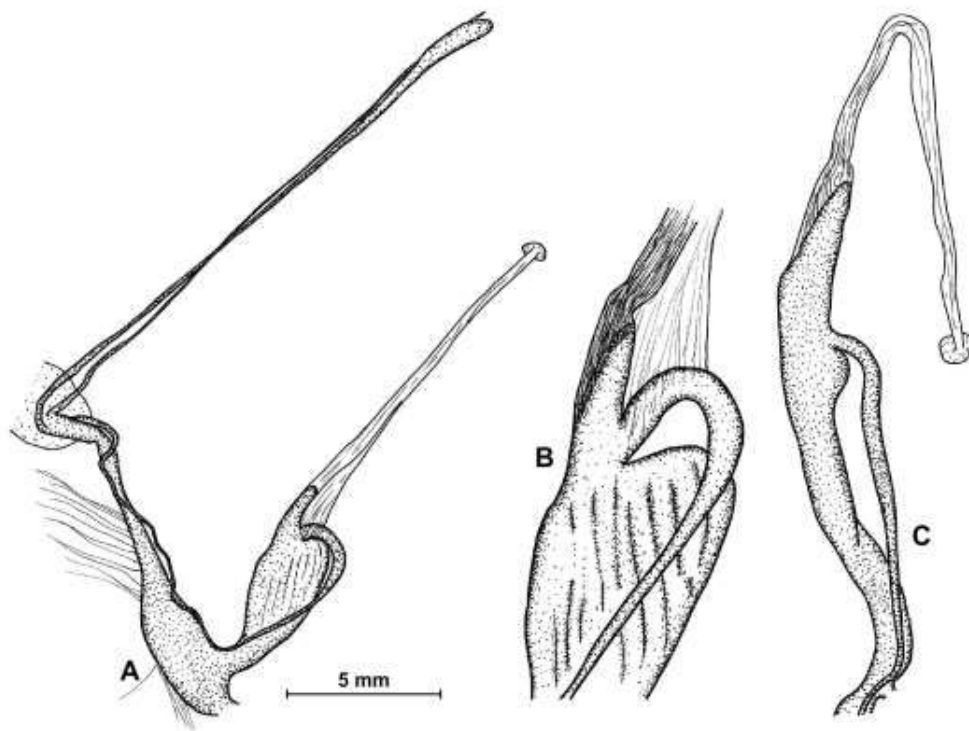


Figure 7.73: *Gudeodiscus (Veludiscus) emigrans otanii* Páll-Gergely & Hunyadi 2013

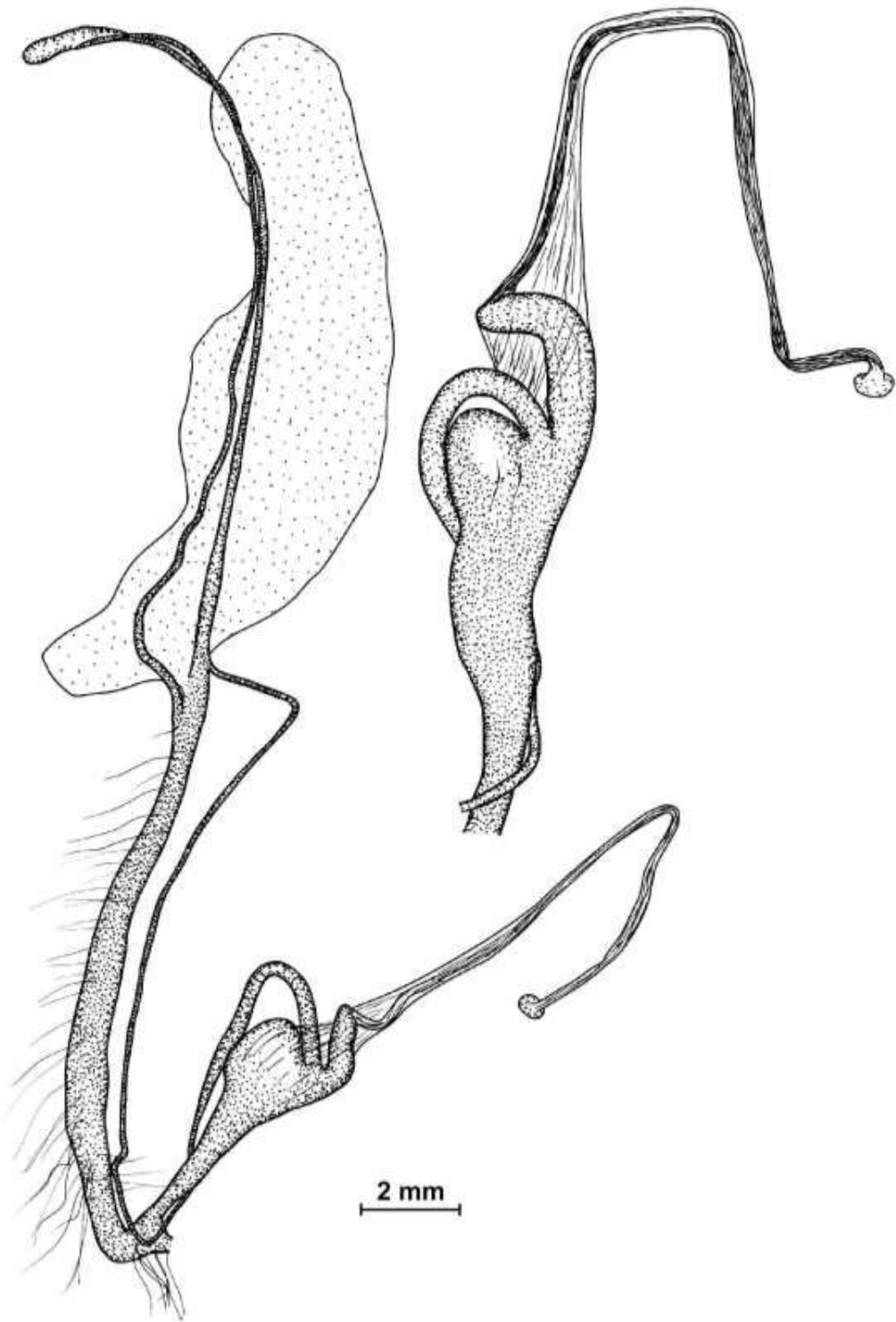


Figure 7.74: *Gudeodiscus (Veludiscus) eroessi* Páll-Gergely & Hunyadi 2013

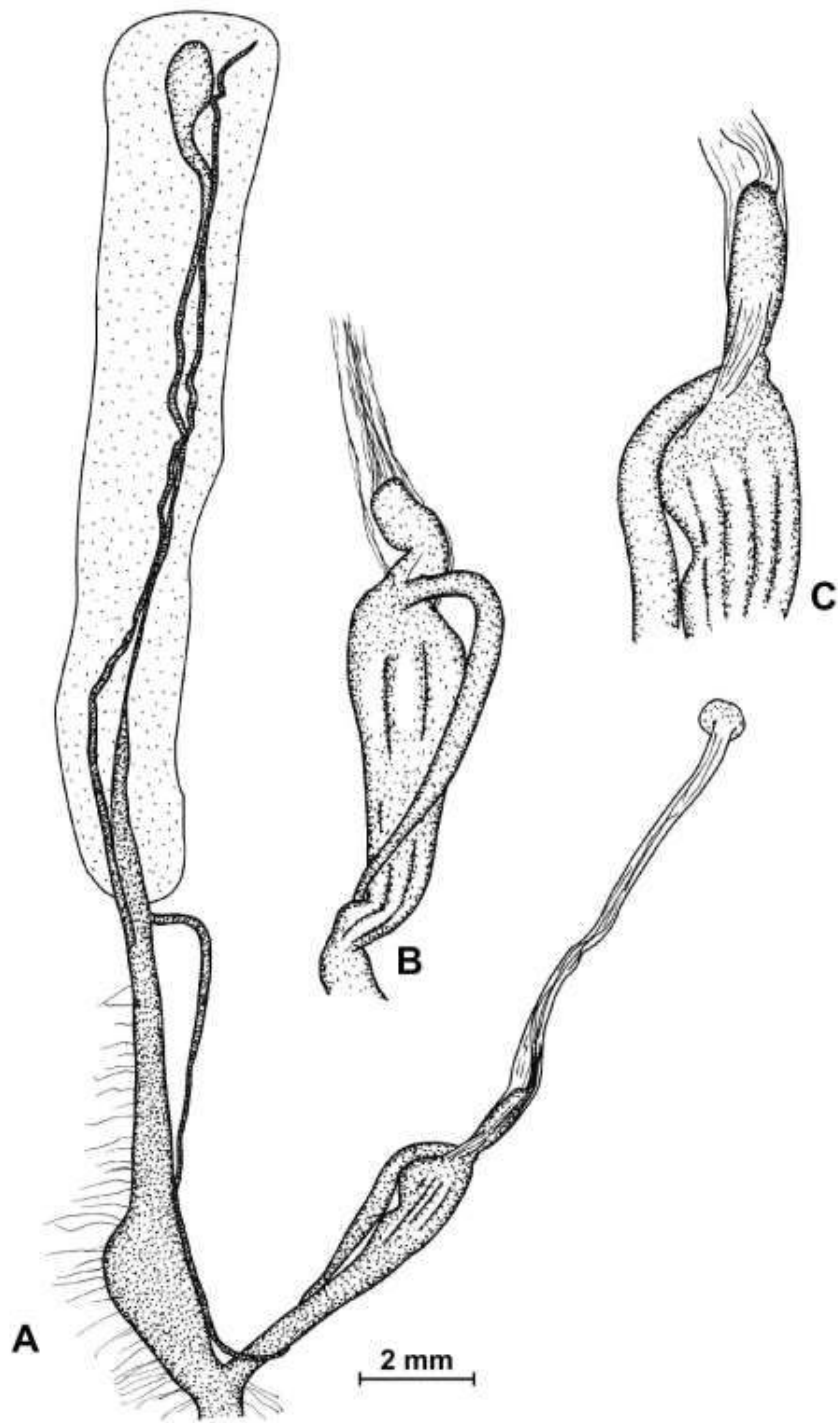


Figure 7.75: *Gudeodiscus (Veludiscus) okuboi* Páll-Gergely & Hunyadi 2013

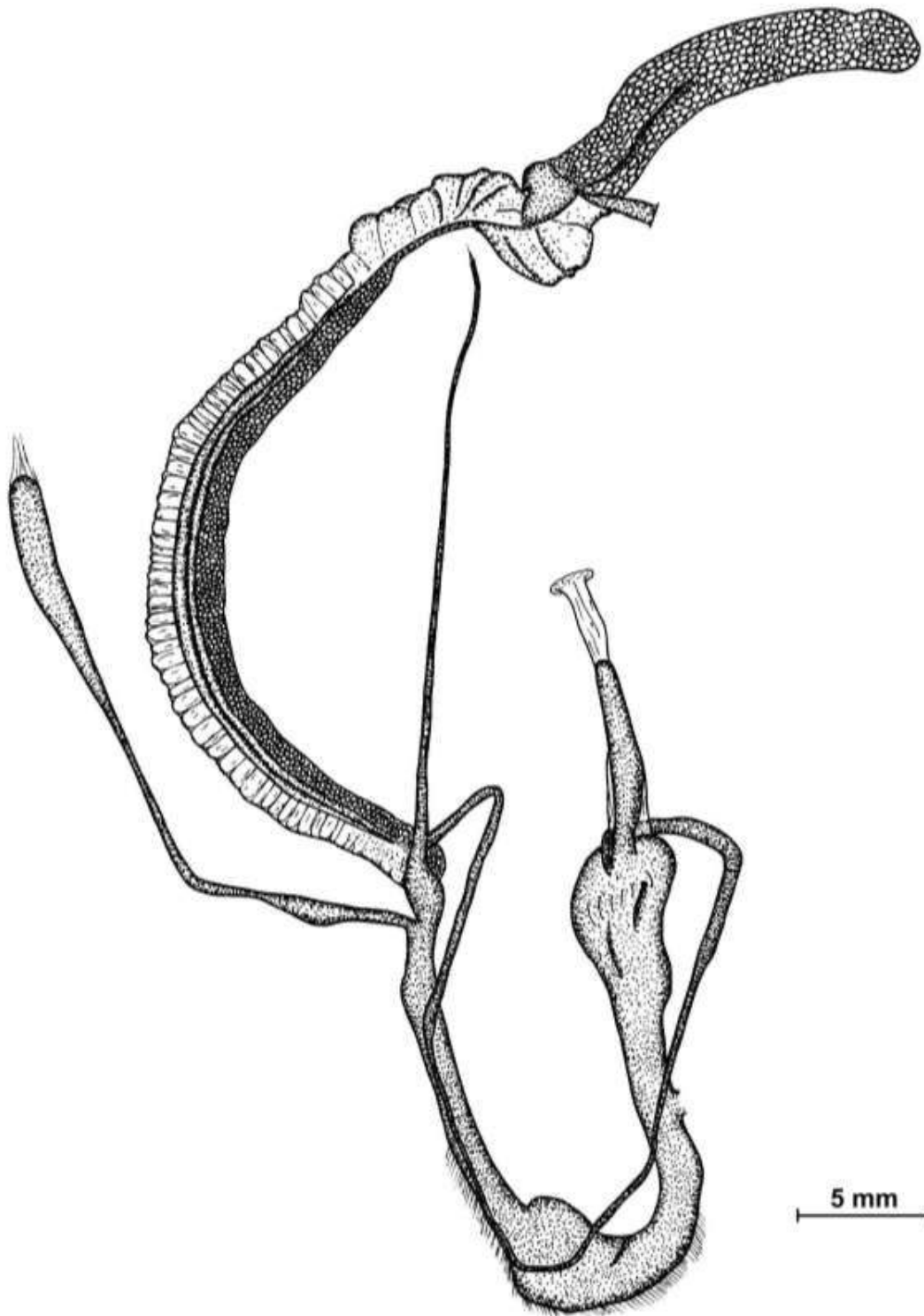


Figure 7.76: *Gudeodiscus (Veludiscus) pulvinaris pulvinaris* (Gould 1859)

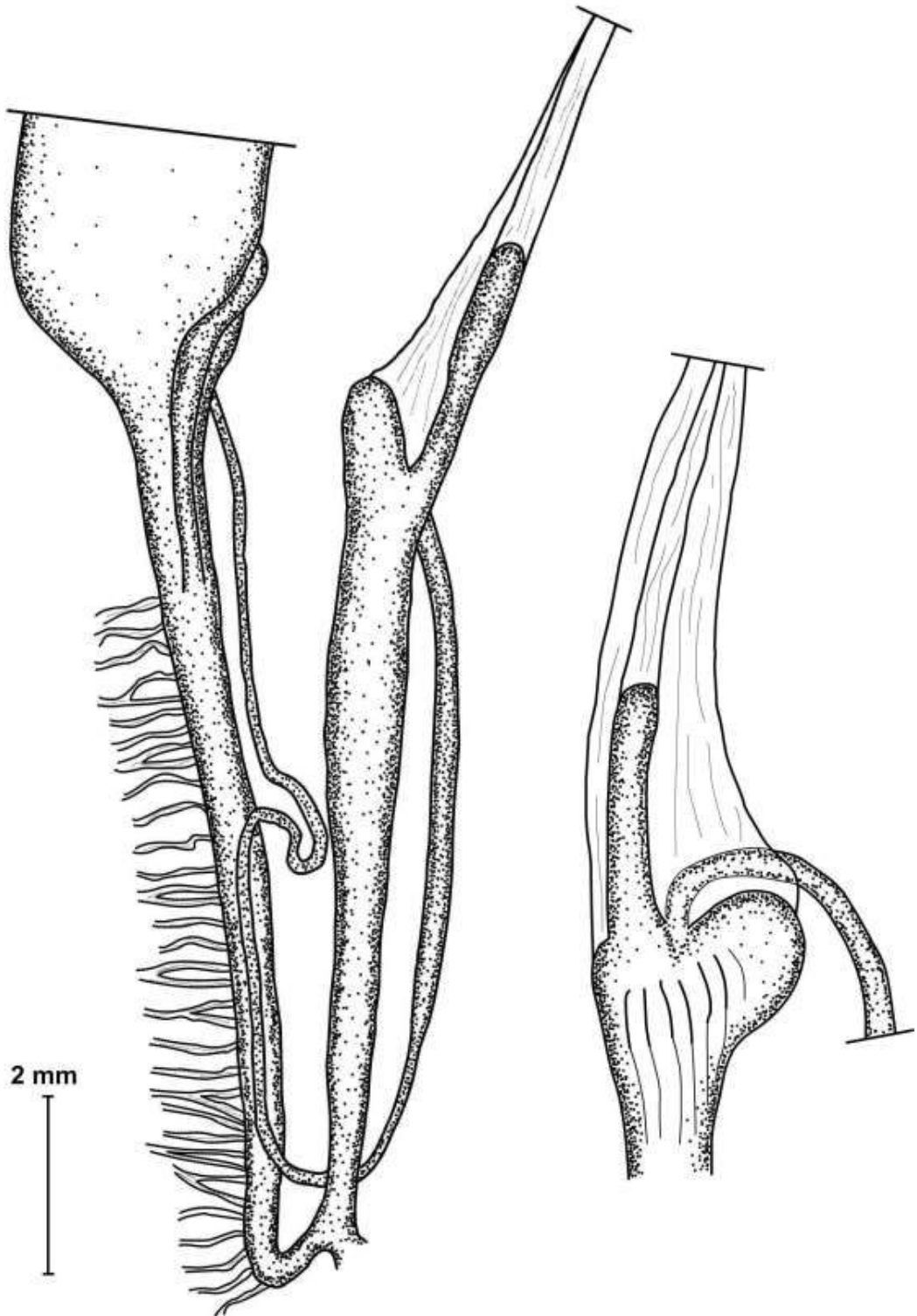


Figure 7.77: *Gudeodiscus (Veludiscus) pulvinaris robustus* Páll-Gergely & Hunyadi 2013

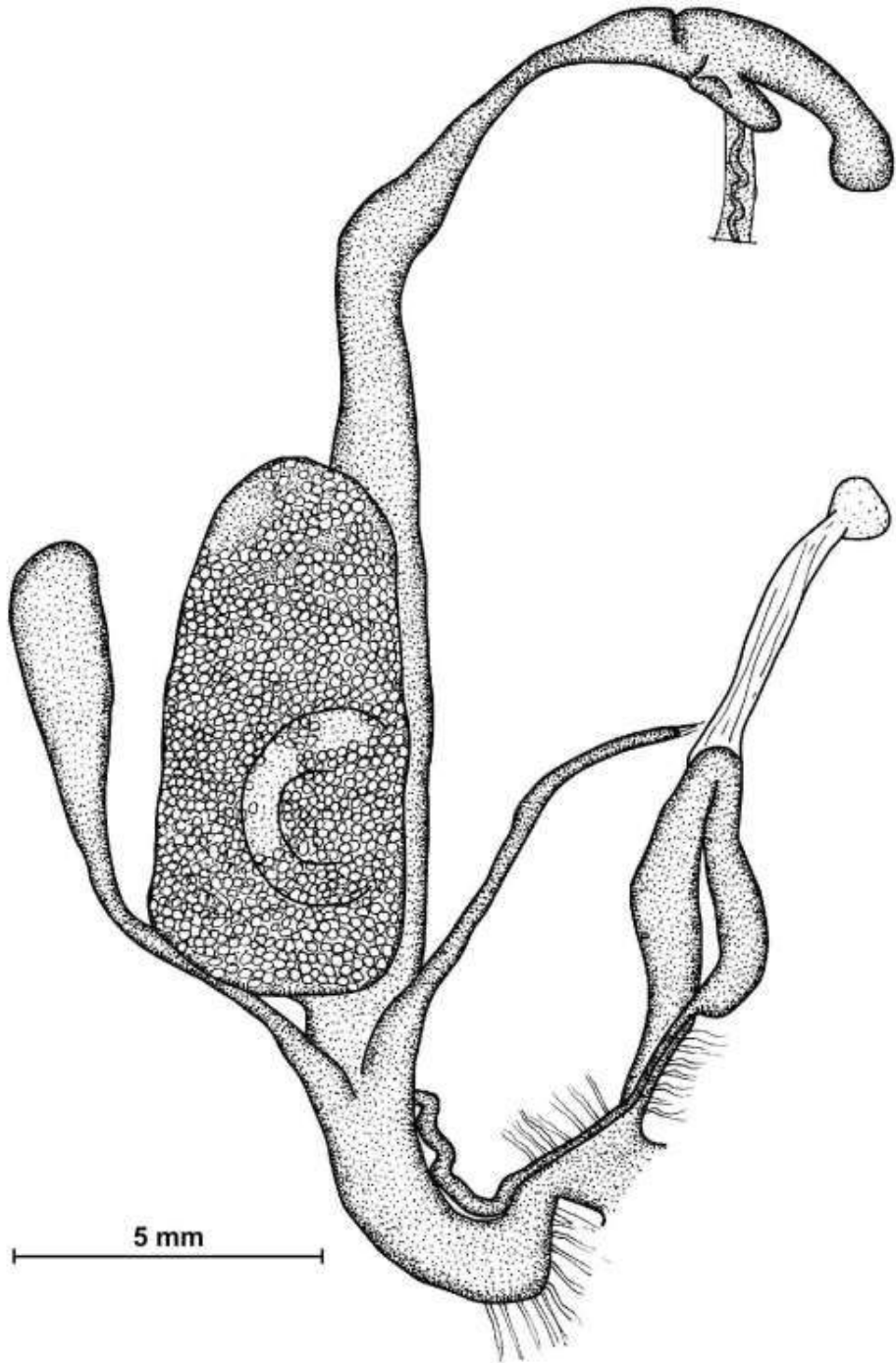


Figure 7.78: *Halongella fruhstorferi* (Möllendorff 1901)

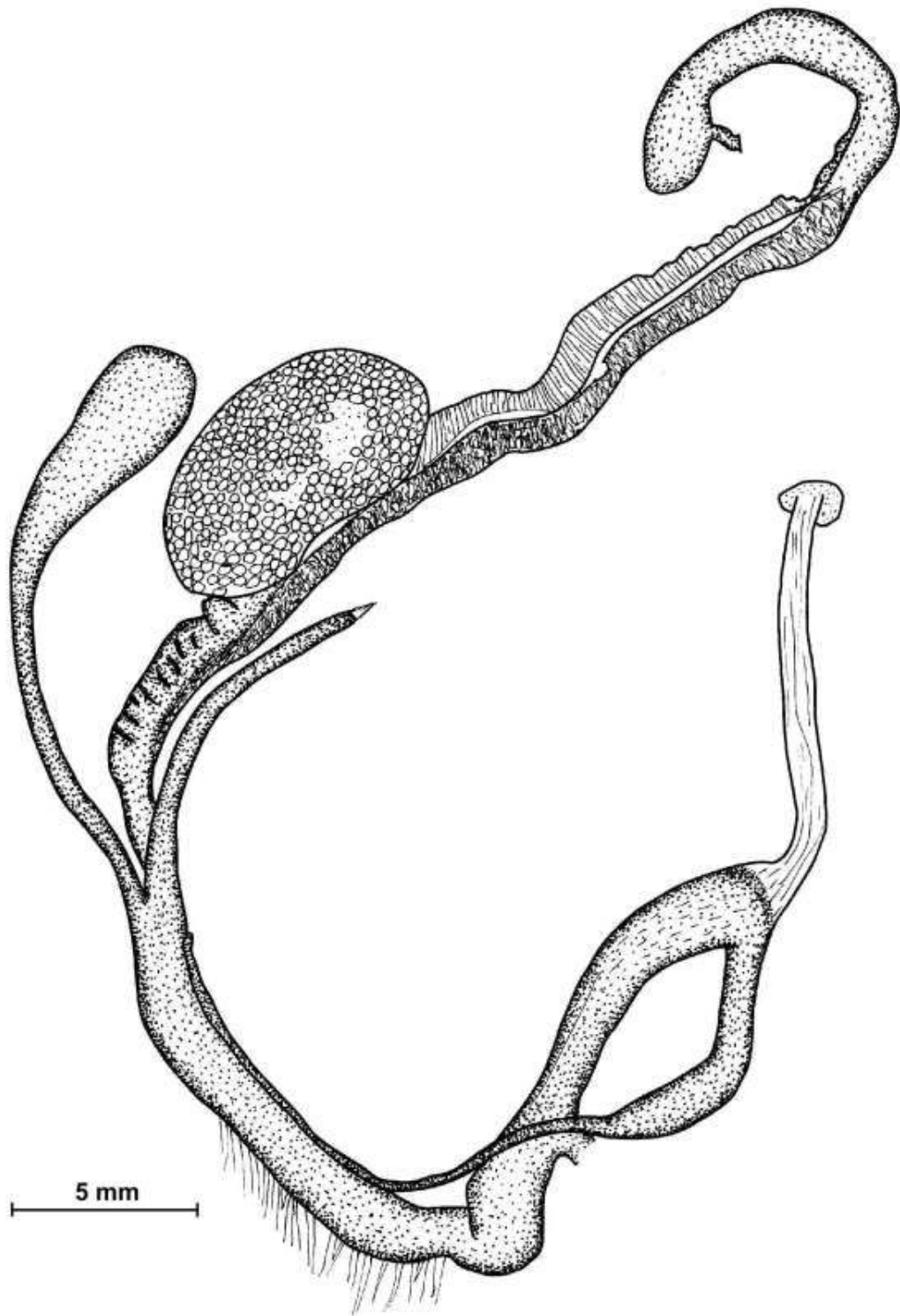


Figure 7.79: *Halongella schlumbergeri* (Morelet 1886)

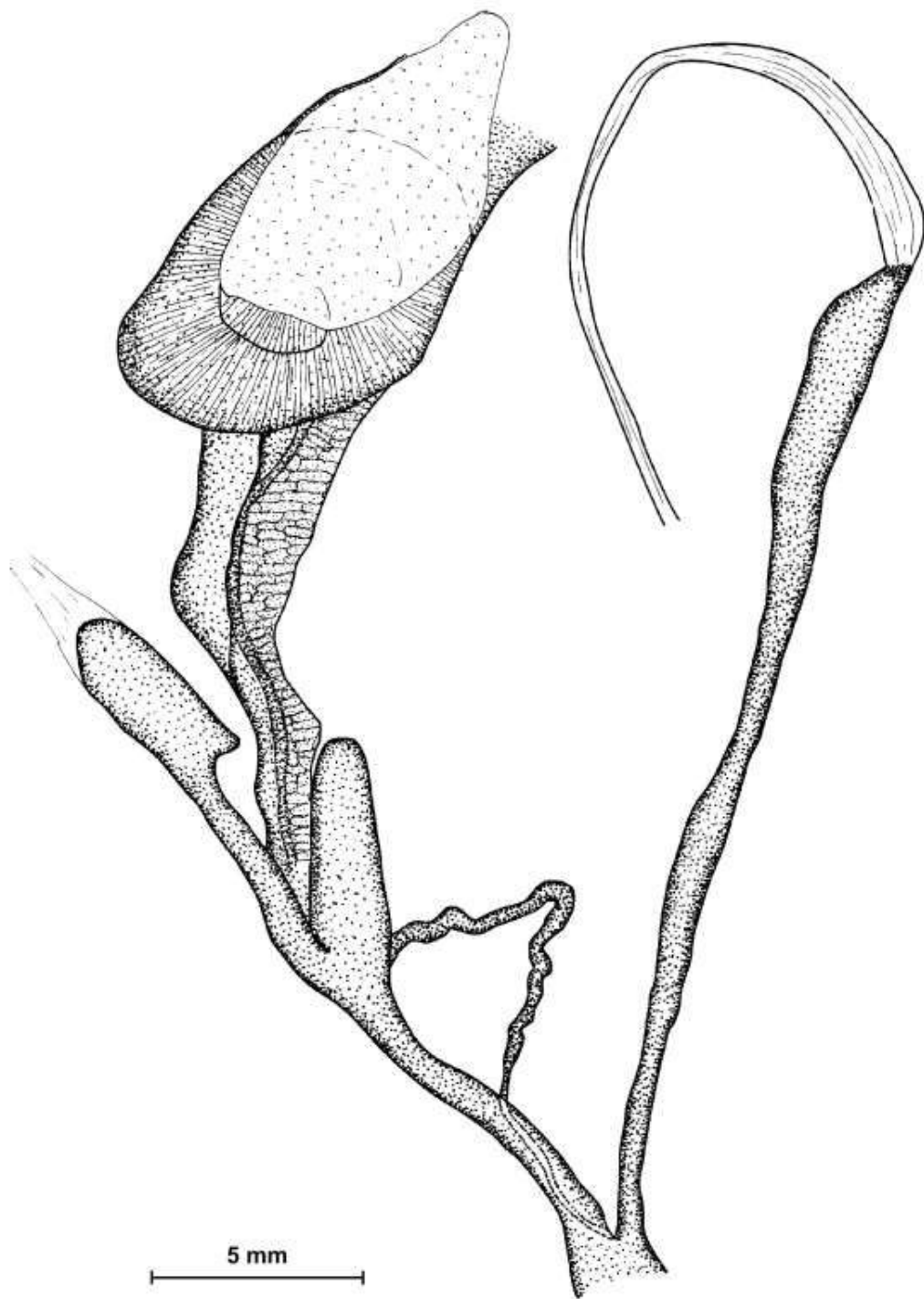


Figure 7.80: Genus3 *laomontana* Pfeiffer 1863

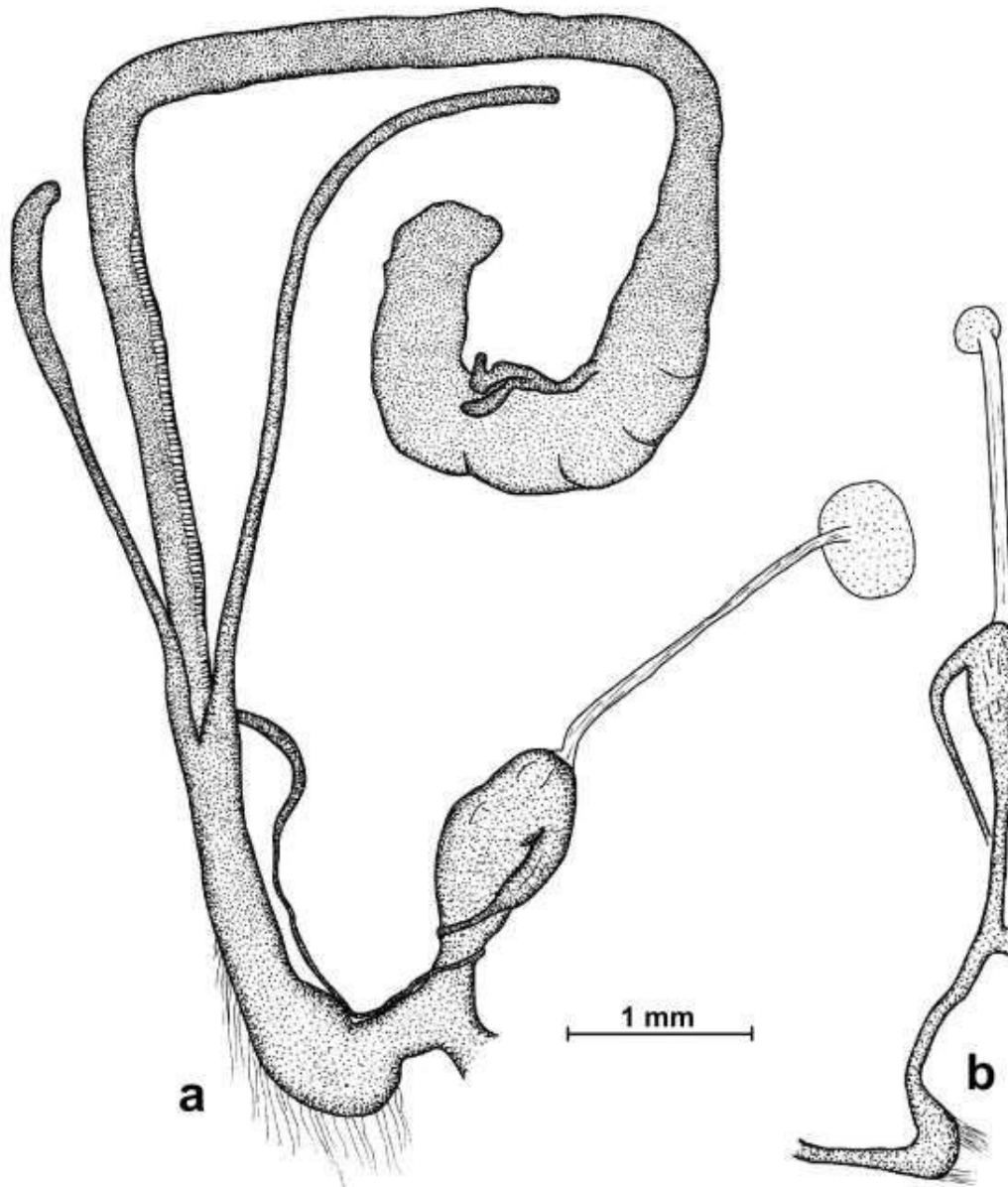


Figure 7.81a: *Sicrodiscus invius* Heude 1885, Figure 7.81b: *Sicrodiscus transitus* Páll-Gergely 2013
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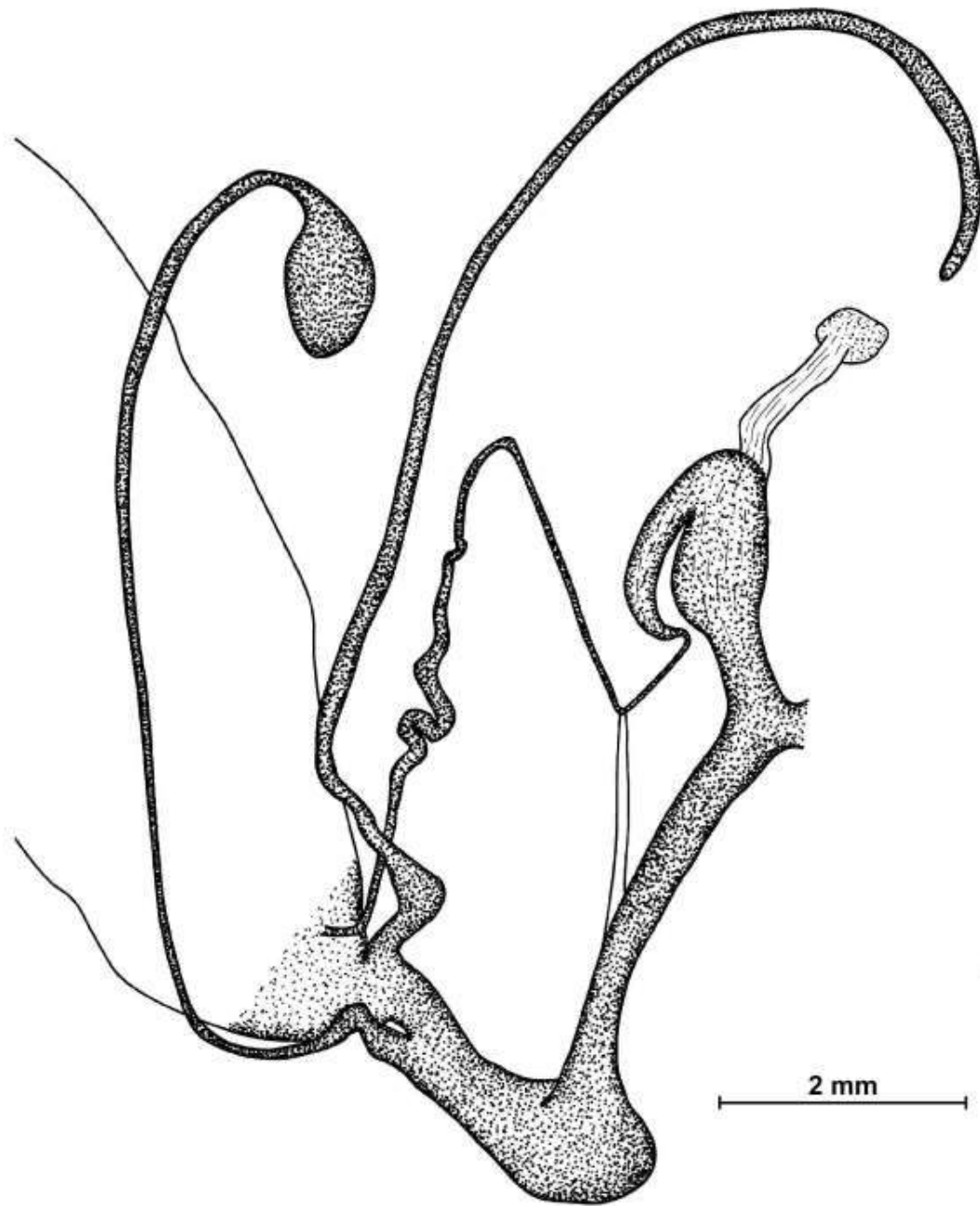


Figure 7.82: *Sicradiscus mansuyi* Gude 1908

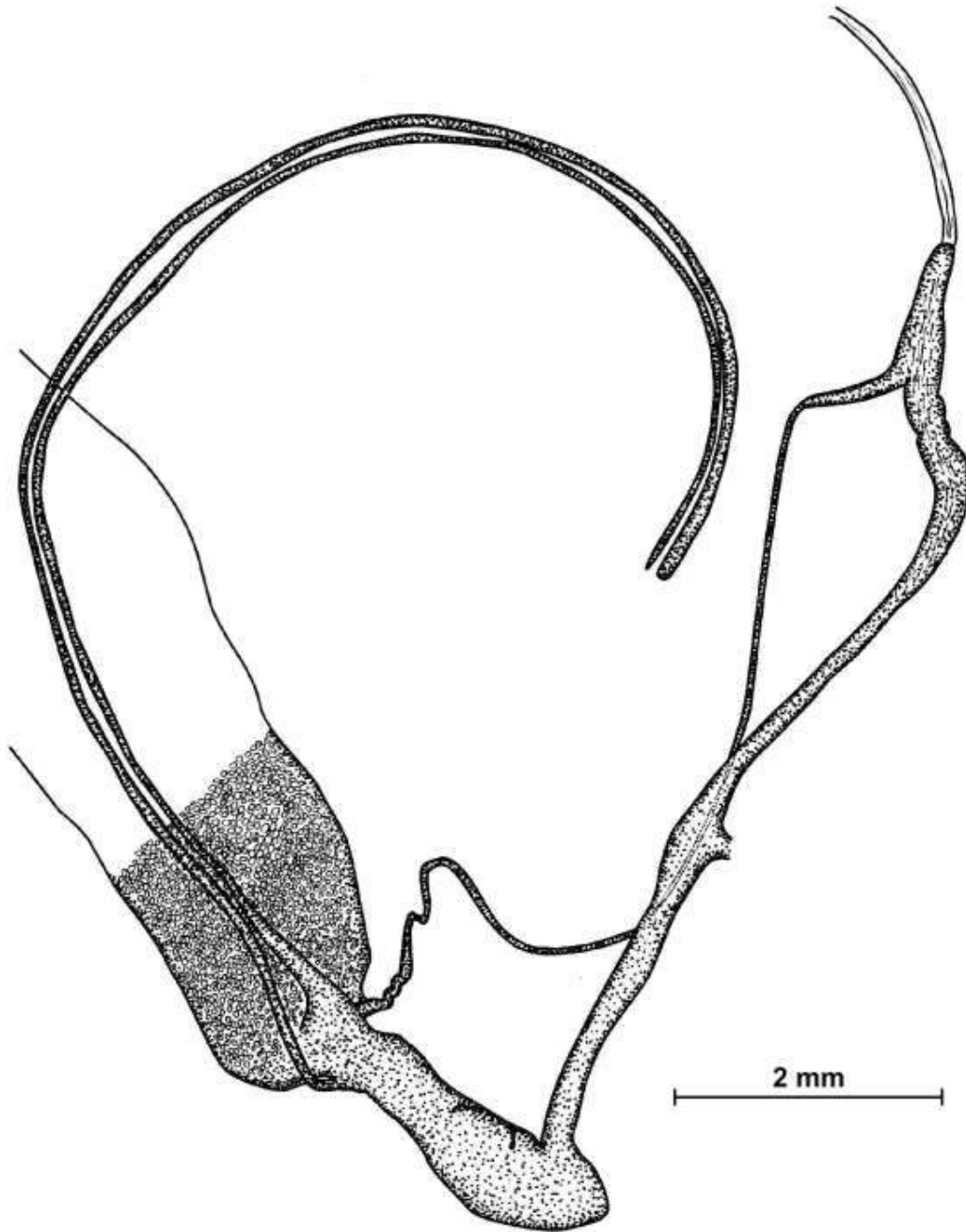


Figure 7.83: *Sicradiscus schistoptychia* Möllendorff 1886

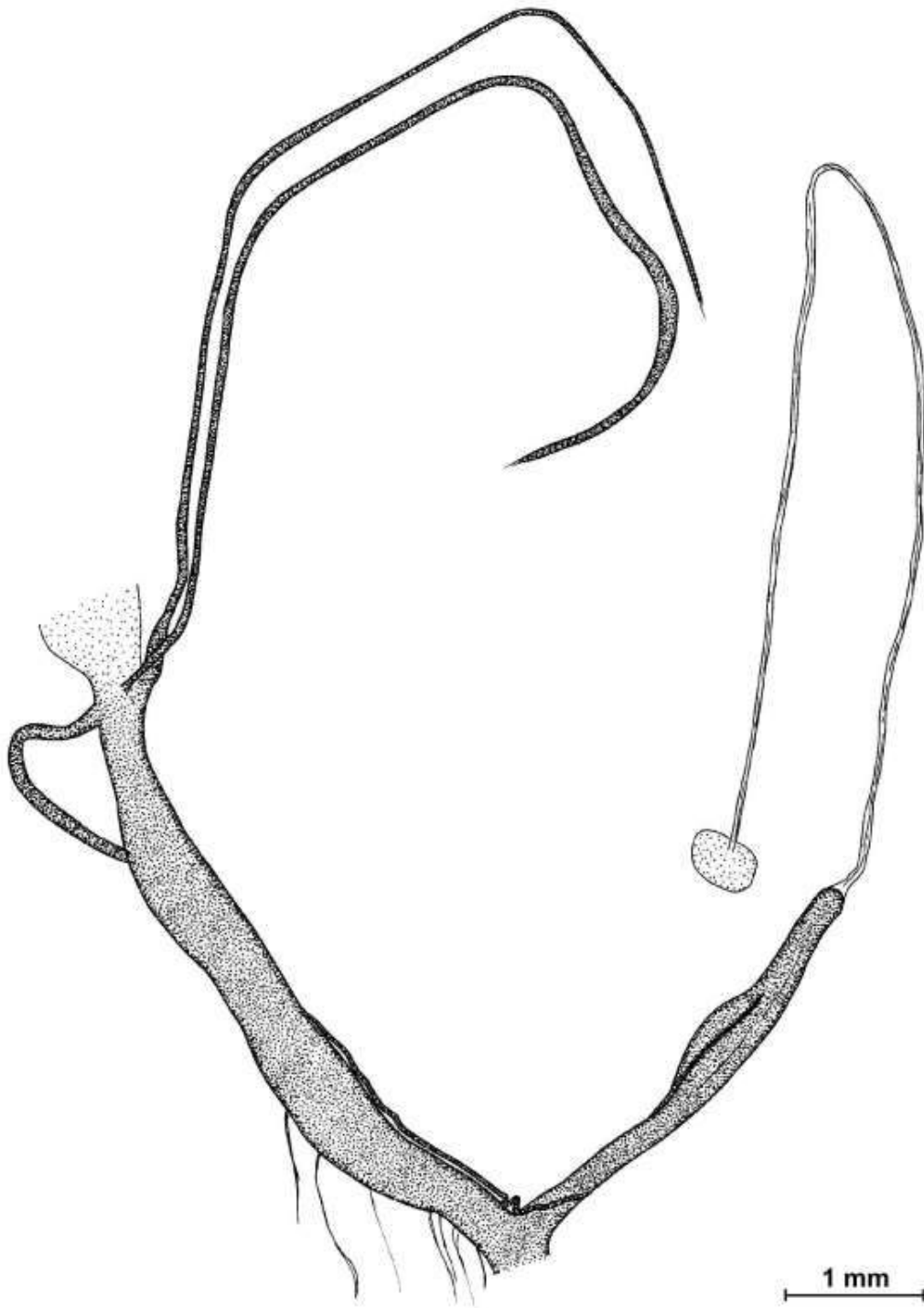


Figure 7.84: *Sinicola asamiana* Páll-Gergely 2013

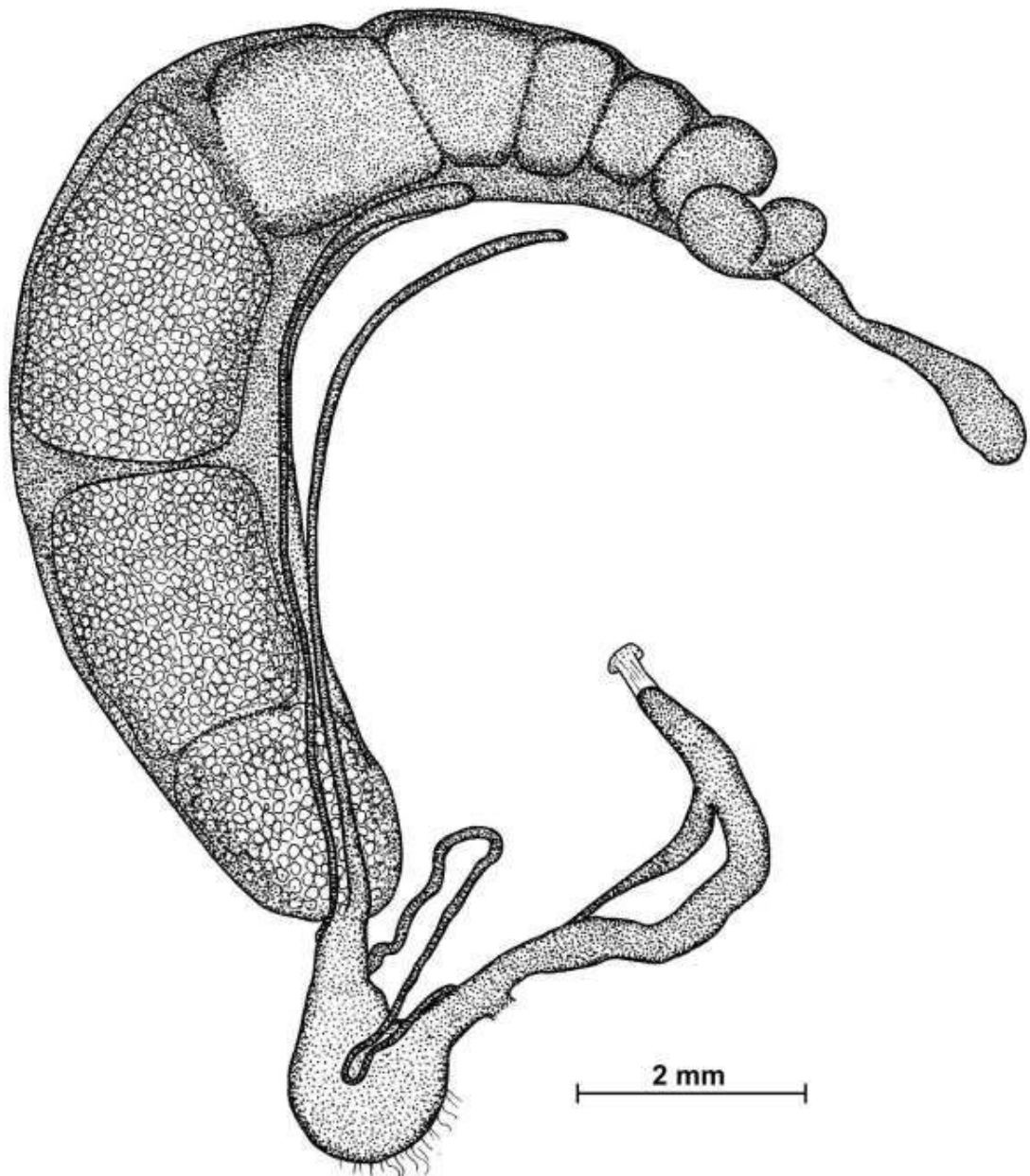


Figure 7.85: *Sinicola emoriens* (Gredler 1881)

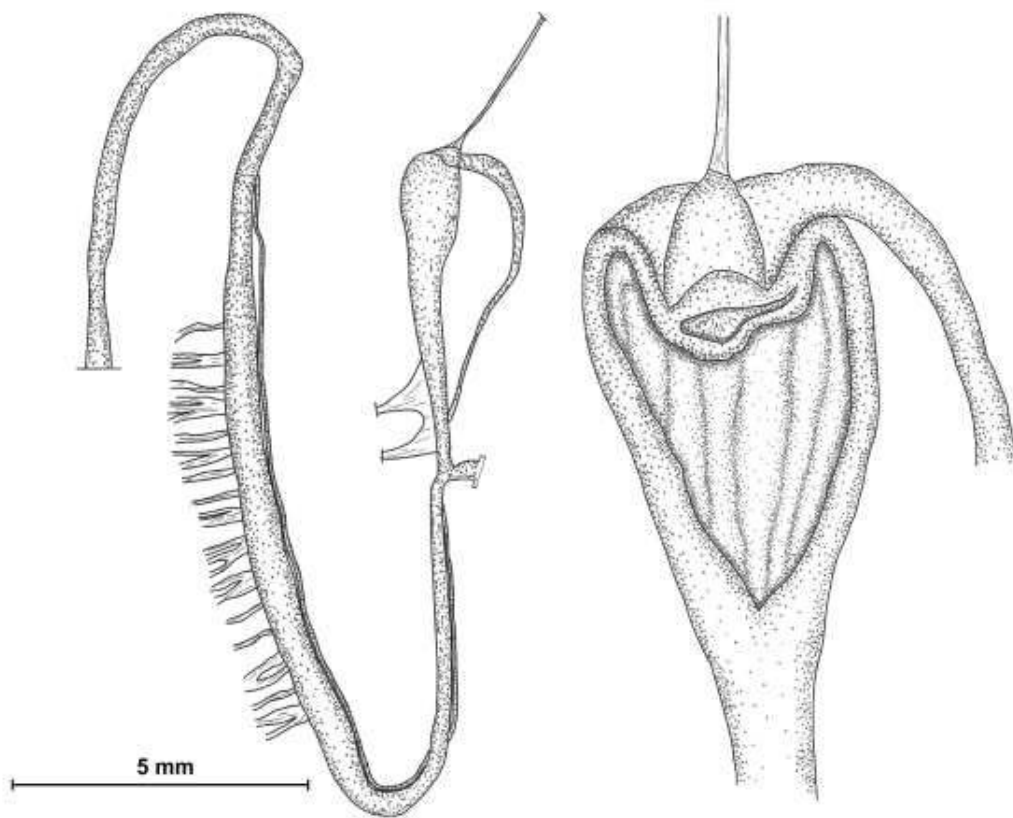


Figure 7.86: *Sinicola fimbriosa* (Martens 1875)

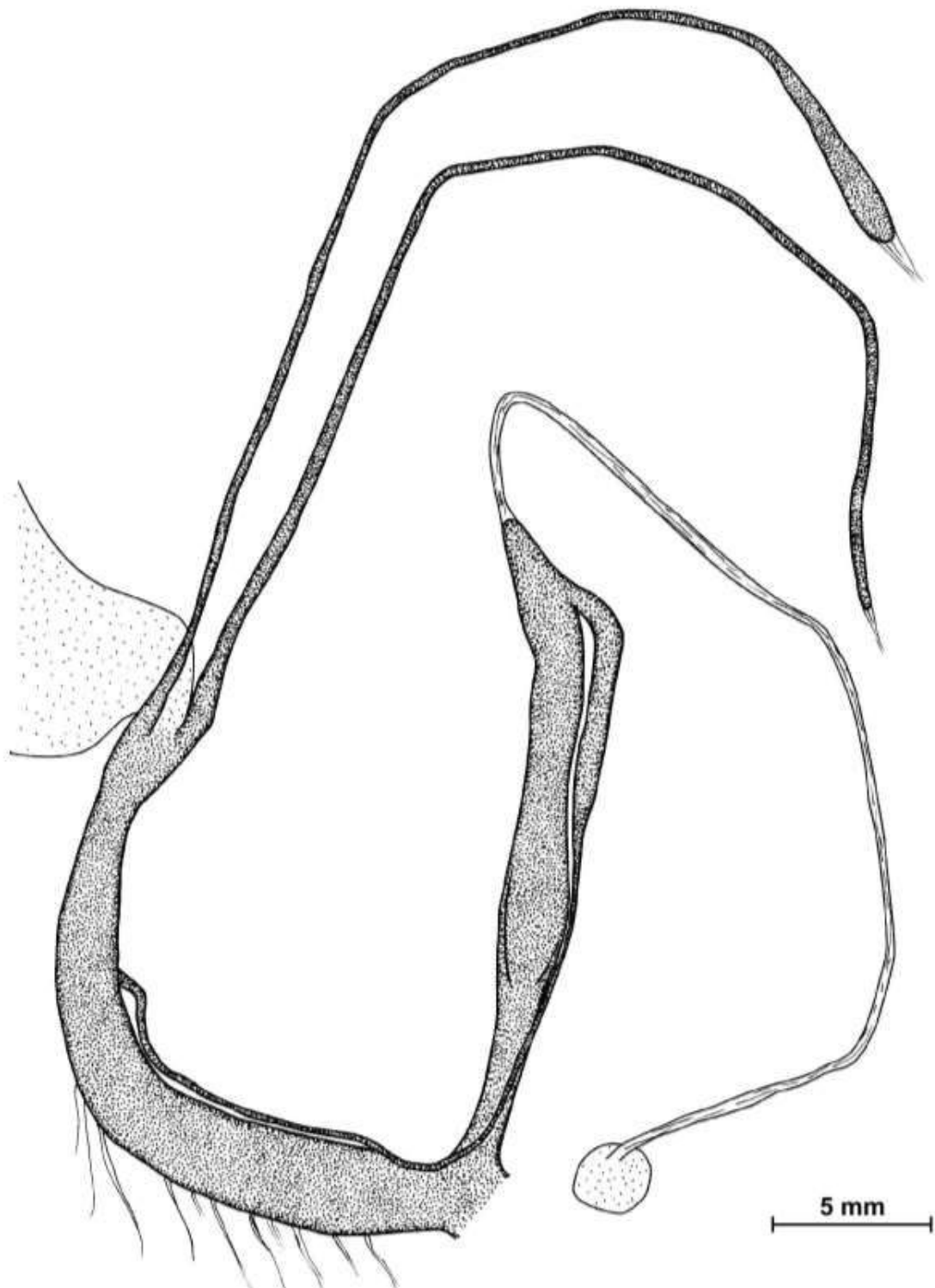


Figure 7.87: *Sinicola murata* (Heude 1885)

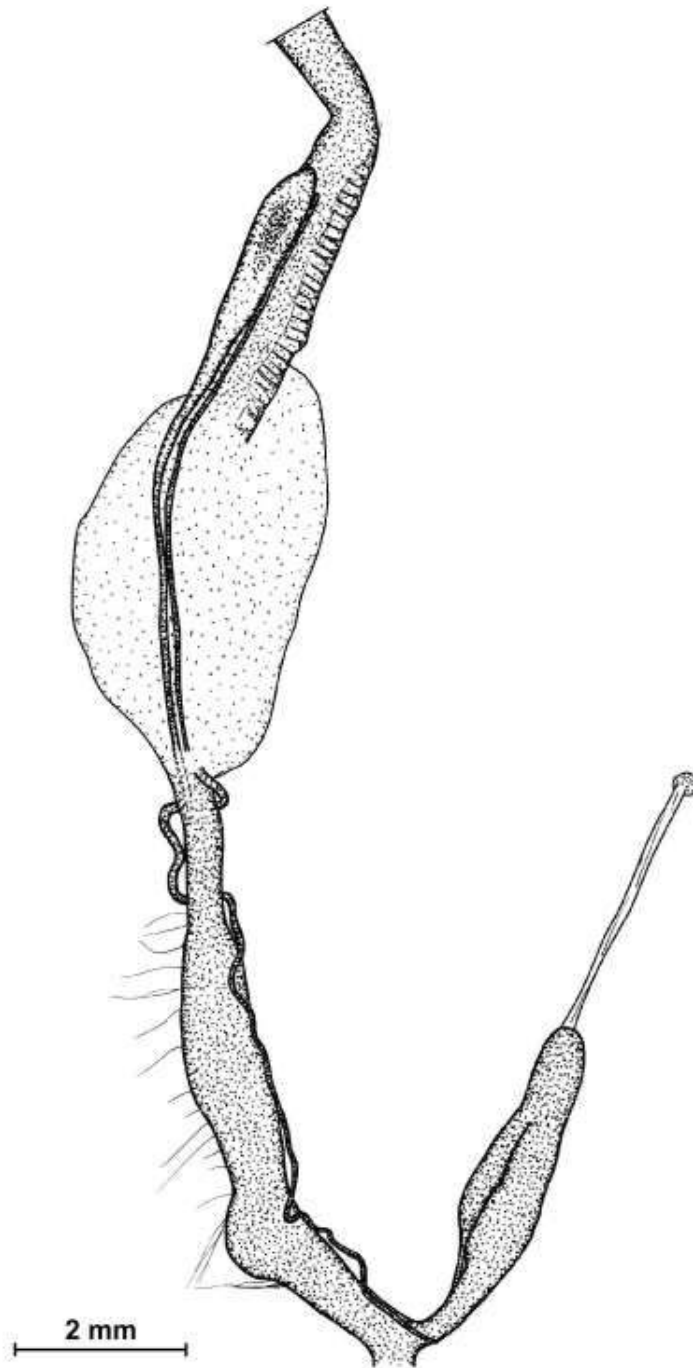


Figure 7.88: *Sinicola reserata azona* (Gredler 1887)

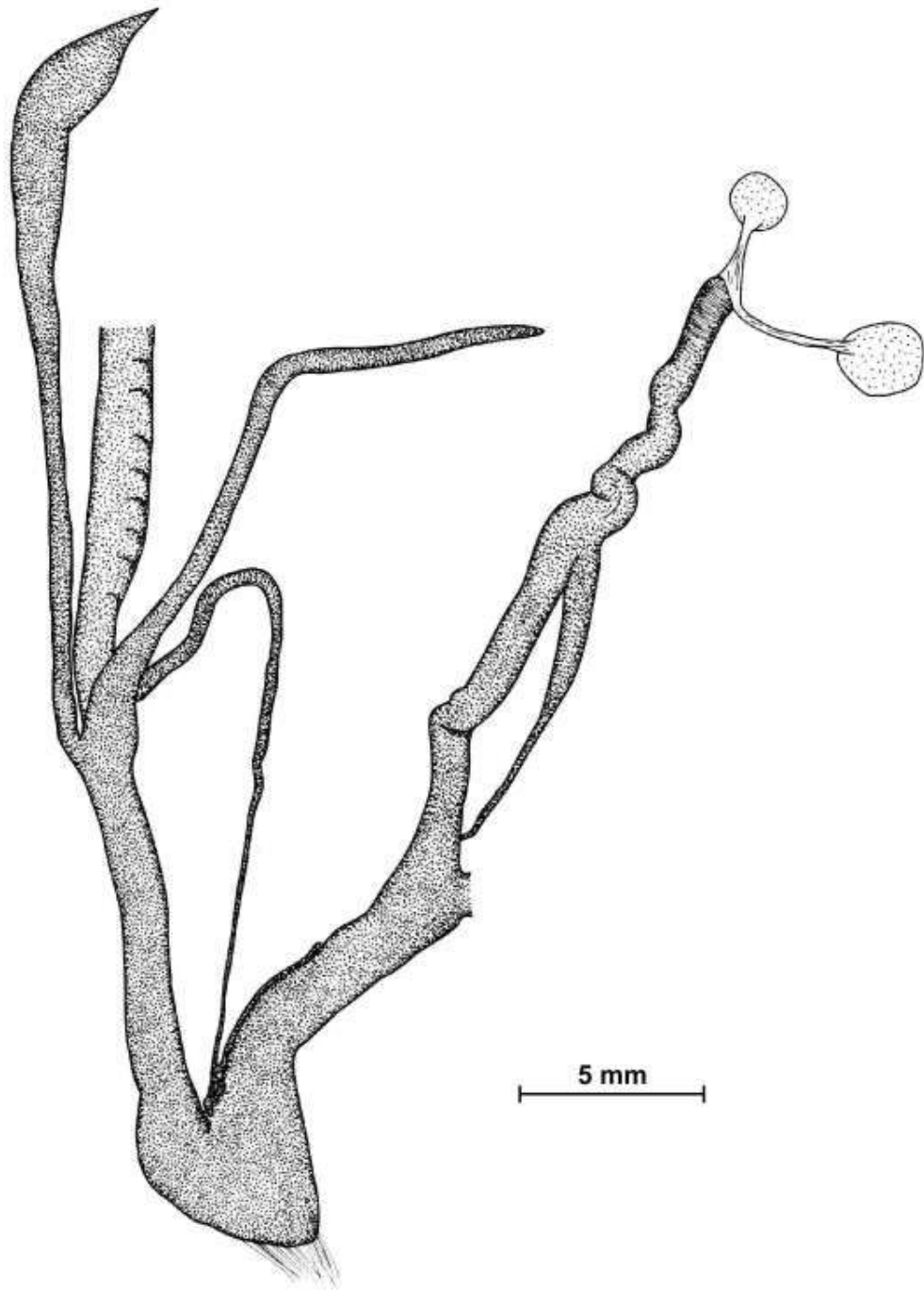


Figure 7.89: *Sinicola stenochila* (Möllendorff 1885)

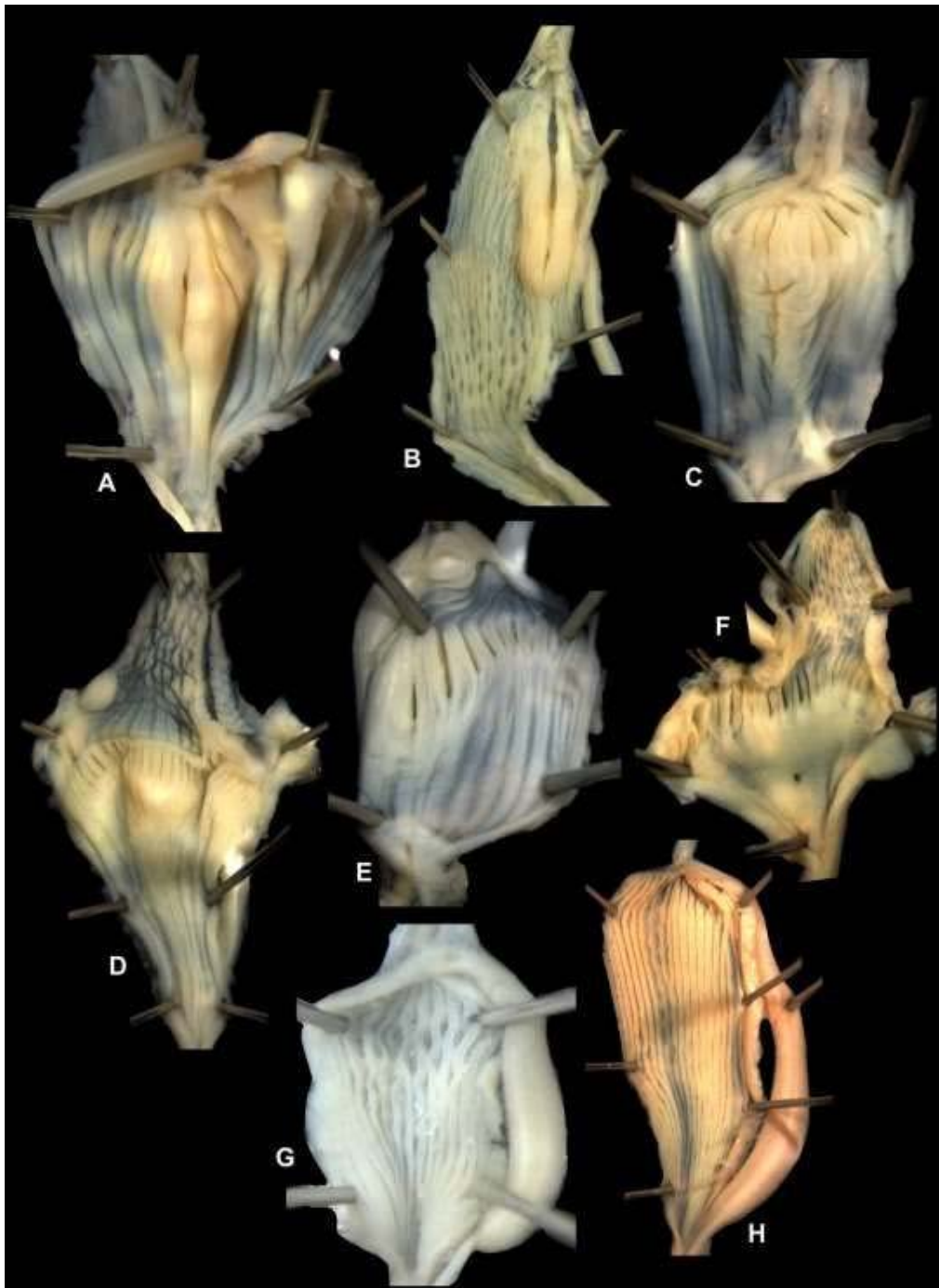


Figure 7.90. Inner walls of the penis of *Gudeodiscus* and *Halongella* species. A: *Gudeodiscus emigrans otanii* Páll-Gergely 2013, 20041113B, "Specimen1"; B: *G. emigrans otanii* Páll-Gergely 2013, 20041113B, "Specimen2"; C: *G. okubo*i Páll-Gergely & Hunyadi 2013, 20041109A, "Specimen1"; D: *G. giardi giardi* (H. Fischer 1898), 20060110E; E: *Gudeodiscus multispira* (Möllendorff 1883), 20041112E; F: *G. eroessi eroessi* Páll-Gergely & Hunyadi 2013, 20041109B, "Specimen1"; G: *Halongella fruhstorferi* (Möllendorff 1901), Vn11-171; H: *Halongella schlumbergeri* (Morlet 1886), 20071122D.

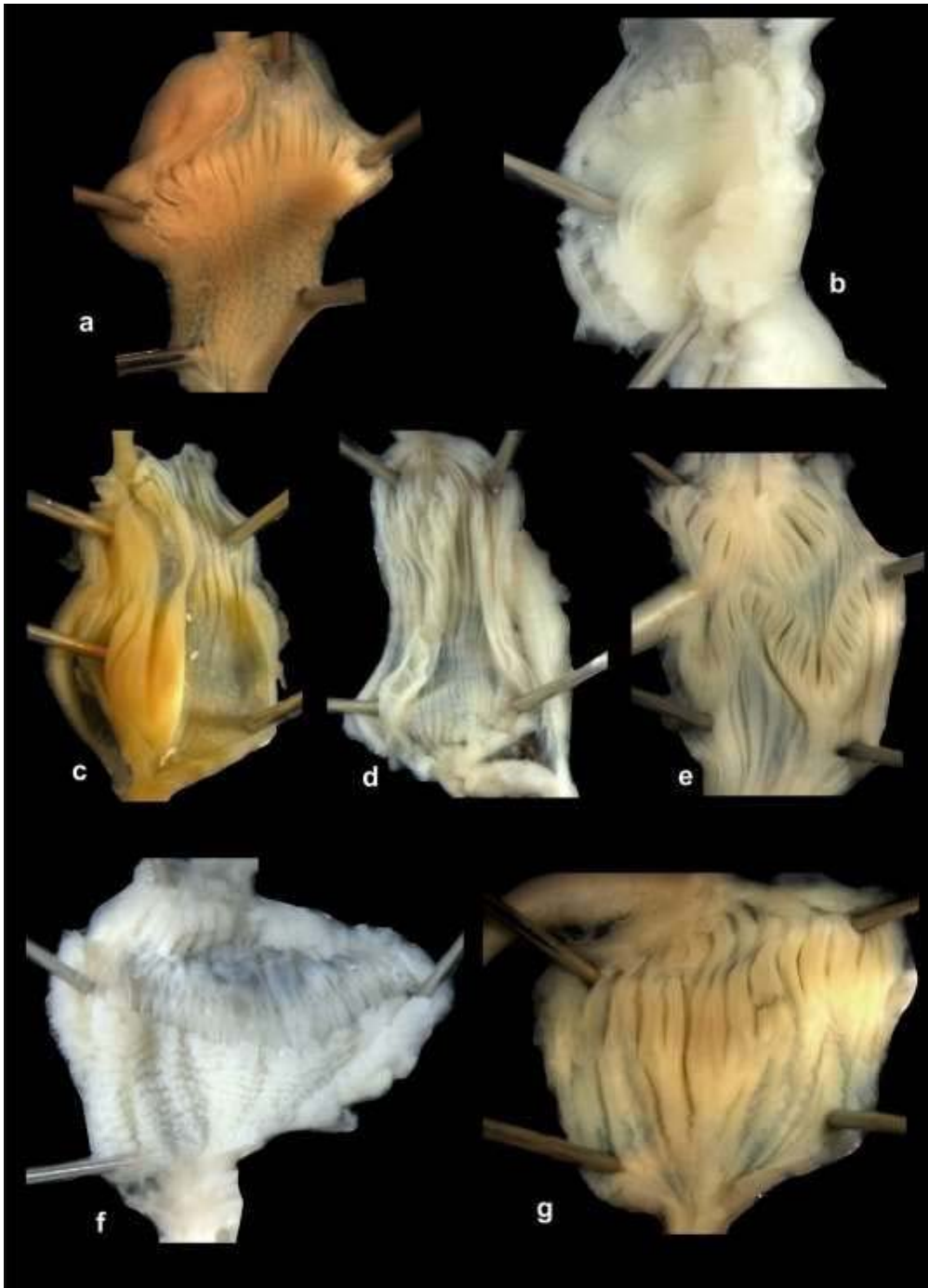


Figure 7.91. Inner walls of the penis of *Gudeodiscus* species. A: *Gudeodiscus (Gudeodiscus) phlyarius* (Gude 1909) (typical *fallax* specimen, Vn11-187); B: *Gudeodiscus giardi giardi* (Fischer 1898), 2011/87; C: *G. (G.) phlyarius* (Mabille 1887), Vn11-156; D: *G. (G.) fischeri* (Gude 1901), Vn11-138; E: *G. (G.) messengeri raheemi* Páll-Gergely & Hunyadi u. ssp., 20080510A; F–G: *G. (G.) villedaryi* specimens collected at the same locality in two different dates: F: November (2011/102) and G: May (20090520A).

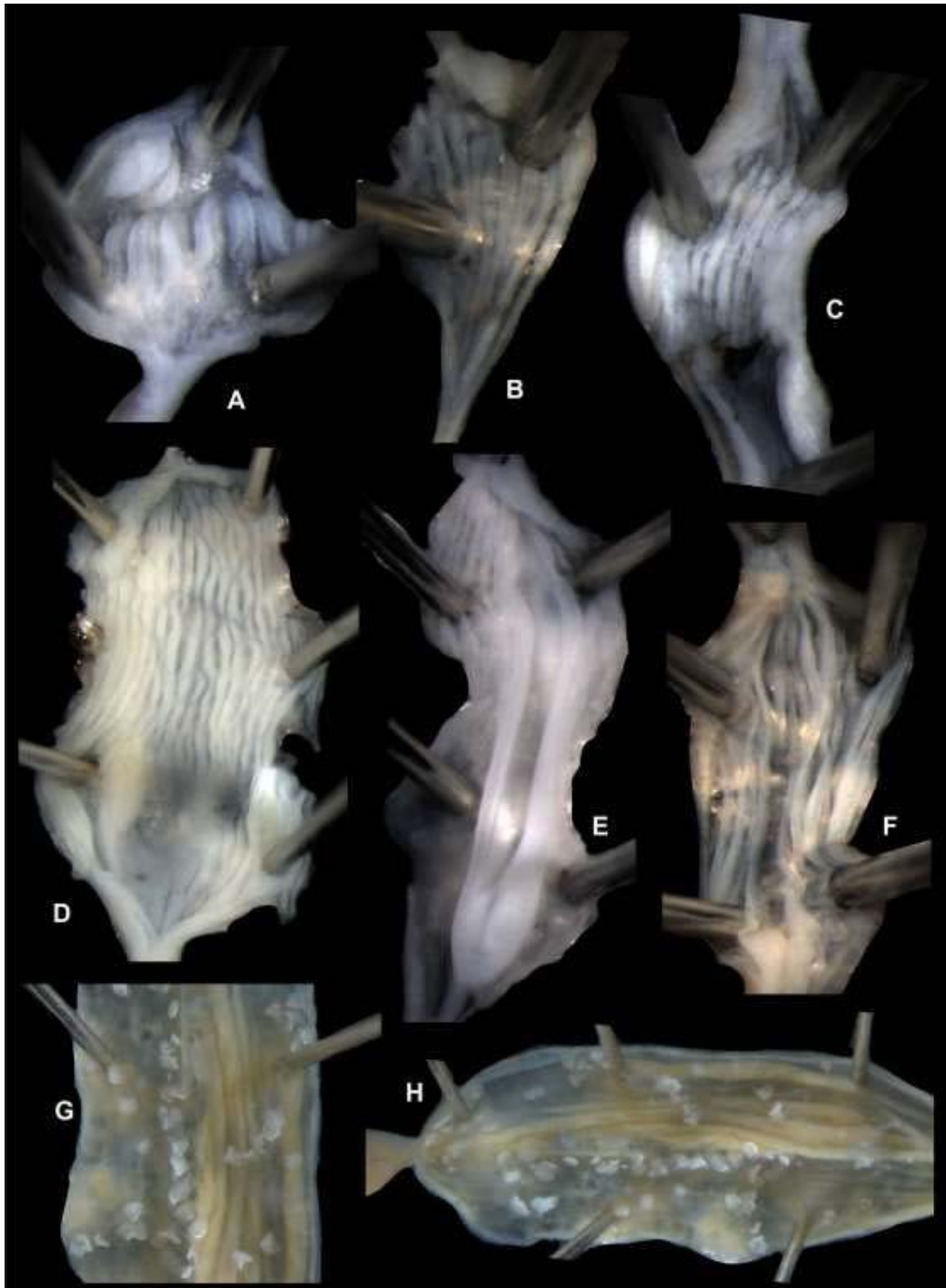


Figure 7.92. Inner walls of the penis of *Sicradiscus*, *Sinicola* and Genus3 species. A: *Sicradiscus invius* (Heude 1885), 20130917A; B: *Sic. transitus* Páll-Gergely 2013, 2013/8; C: *Sin. asamiana* Páll-Gergely 2013, 20130916A; D: *Sin. reserata azona* (Gredler 1887), 20090308B; E: *Sin. murata* (Heude 1885), 20130916A; F: *Sin. emoriens* (Gredler 1881), 2010/41; Genus3 *laomontana*.

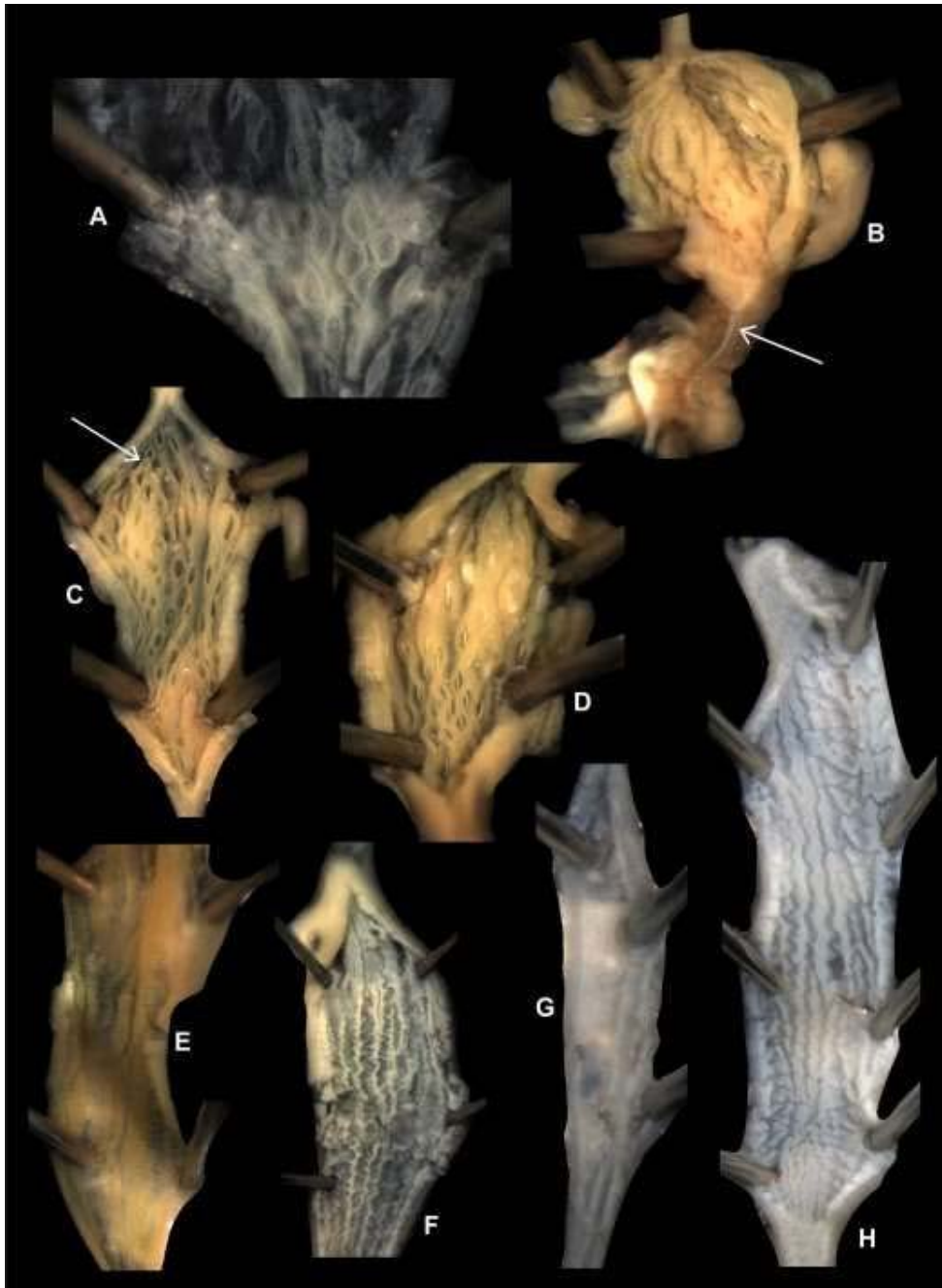


Figure 7.93. A: *Endothyrella fultoni* (Godwin-Austen 1892), Khasi, leg. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.598.; B–D: *Endothyrella plectostoma* (Benson 1836), Sikkim, leg. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.451; E: *Plectopylis* species2; F: *Plectopylis bensoni*; G: *Ch. perrierae*; H: *Chersaecia shanensis*. Arrow on Fig. B. shows the entering point of the vas deferens to the penis. Arrow on Fig. C shows rounded calcareous granules.

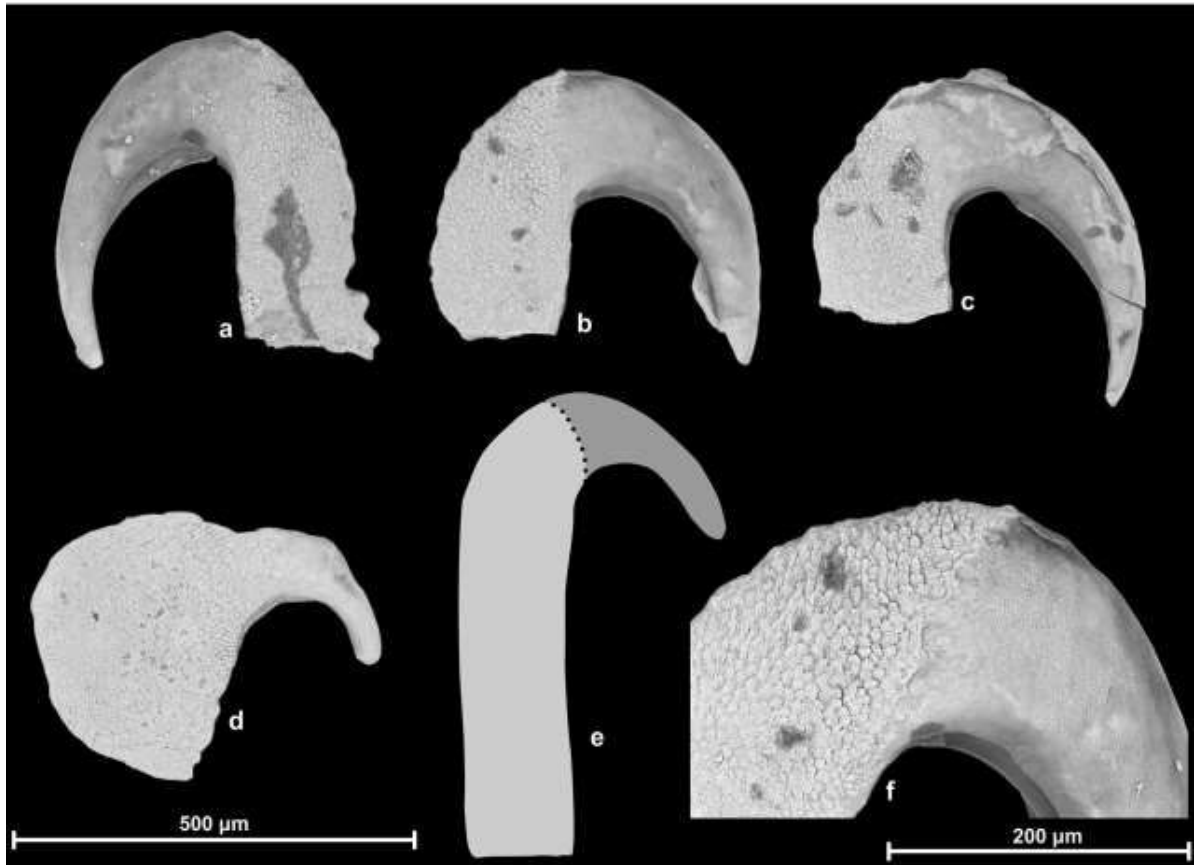


Figure 7.94. Calcareous claws found in pockets on the inner penial wall of *Gudeodiscus* and *Halongella* species. A–C, F: *Gudeodiscus (Gudeodiscus) villedaryi* (Ancey 1888) (for locality see Figure 23); D: *Gudeodiscus giardi giardi* (Fischer 1898) (for locality see Figure 19); E: *G. (G.) fischeri* (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 a drawings are presented.

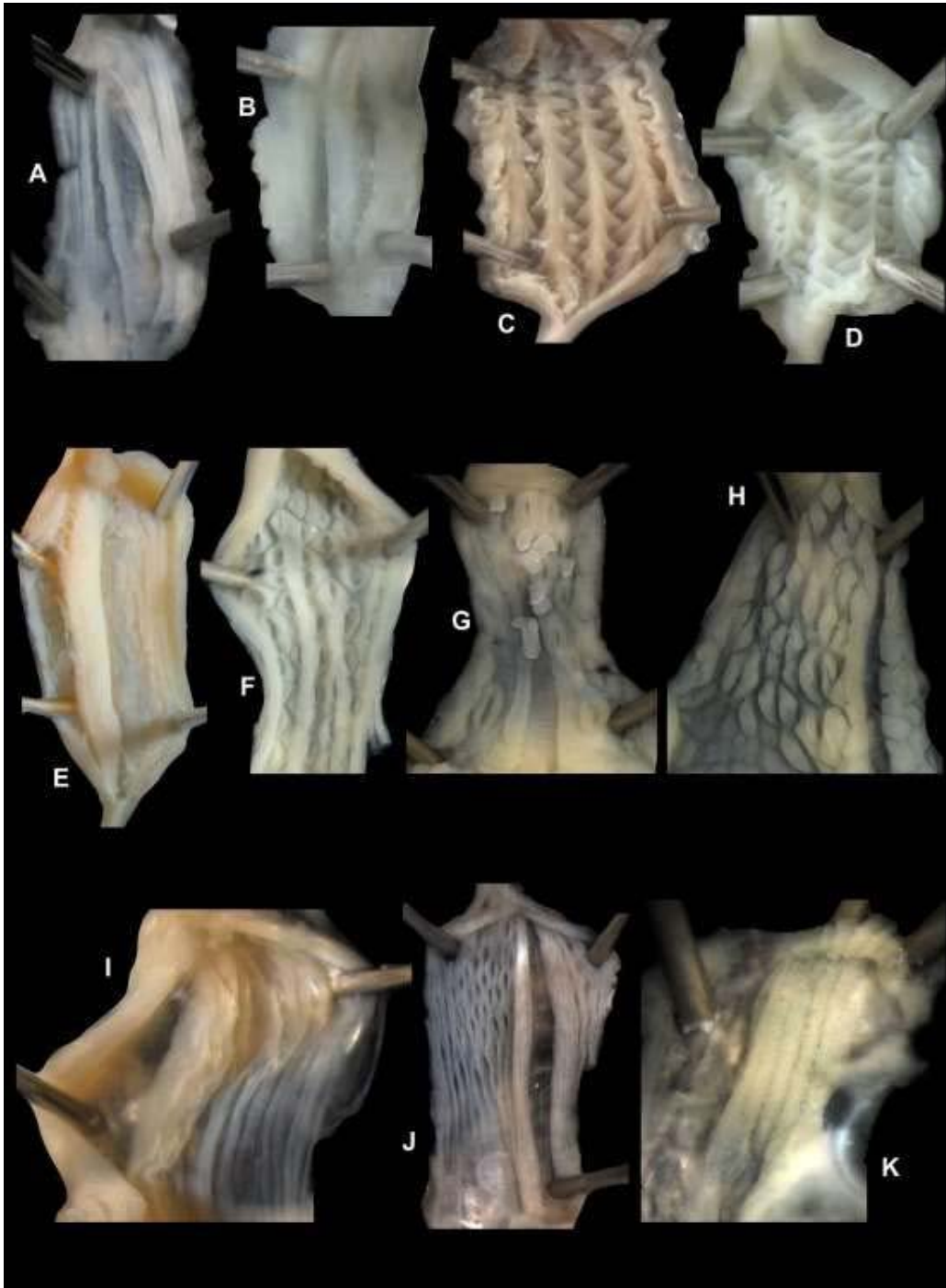


Figure 7.95. Inner wall of the epiphallus (A–E) and the penial caecum (F–K). A: *Gudeodiscus fischeri* (Gude 1901); B: *Gudeodiscus giardi giardi* (Fischer 1898); C: *Halongella schlumbergeri* (Morlet 1886); D: *Halongella fruhstorferi* (Möllendorff 1901), (for locality see Figure 25); E: *Gudeodiscus messengeri raheemi* Laos; F: *G. (G.) messengeri raheemi* Páll-Gergely & Hunyadi u. ssp.; G: *G. (G.) messengeri raheemi* Páll-Gergely & Hunyadi u. ssp.; H: *G. giardi* China; I: *Gudeodiscus pulvinaris pulvinaris*; J: *G. pulvinaris robustus*; K: *Endothyrella fultoni*.

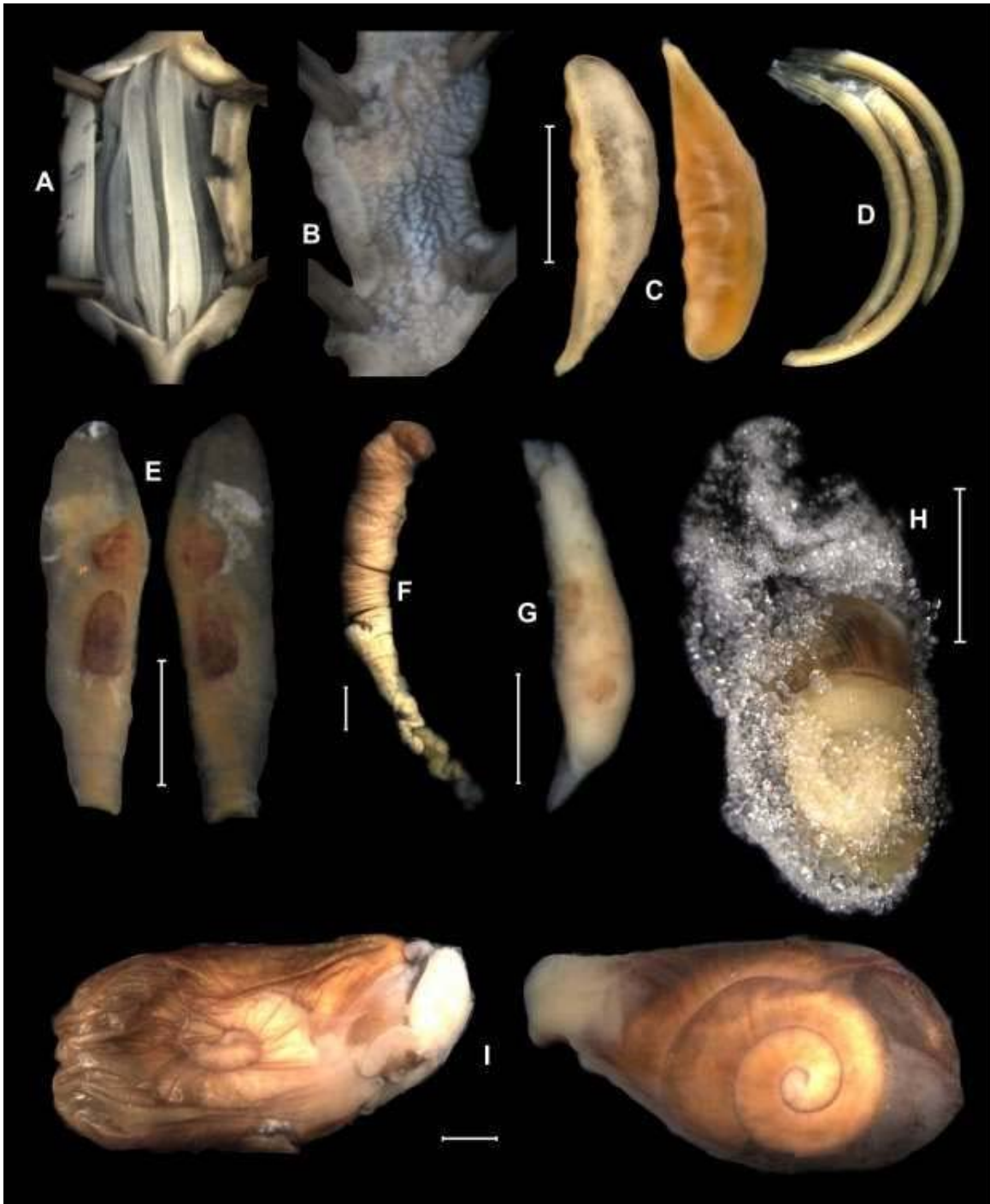


Figure 7.96. Epiphallus (A–B), spermatophore (C–G) and embryos (H–I) of Plectopylidae species. A: *Plectopylis bensoni*; B: *Chersaecia shanensis*; C: *G. emigrans otanii*; D: *G. fischeri*; E: *Sinicola reserata azona*; F: *Plectopylis bensoni*; G: *Chersaecia shanensis*; H: *S. reserata azona*; I: *P. species2*.

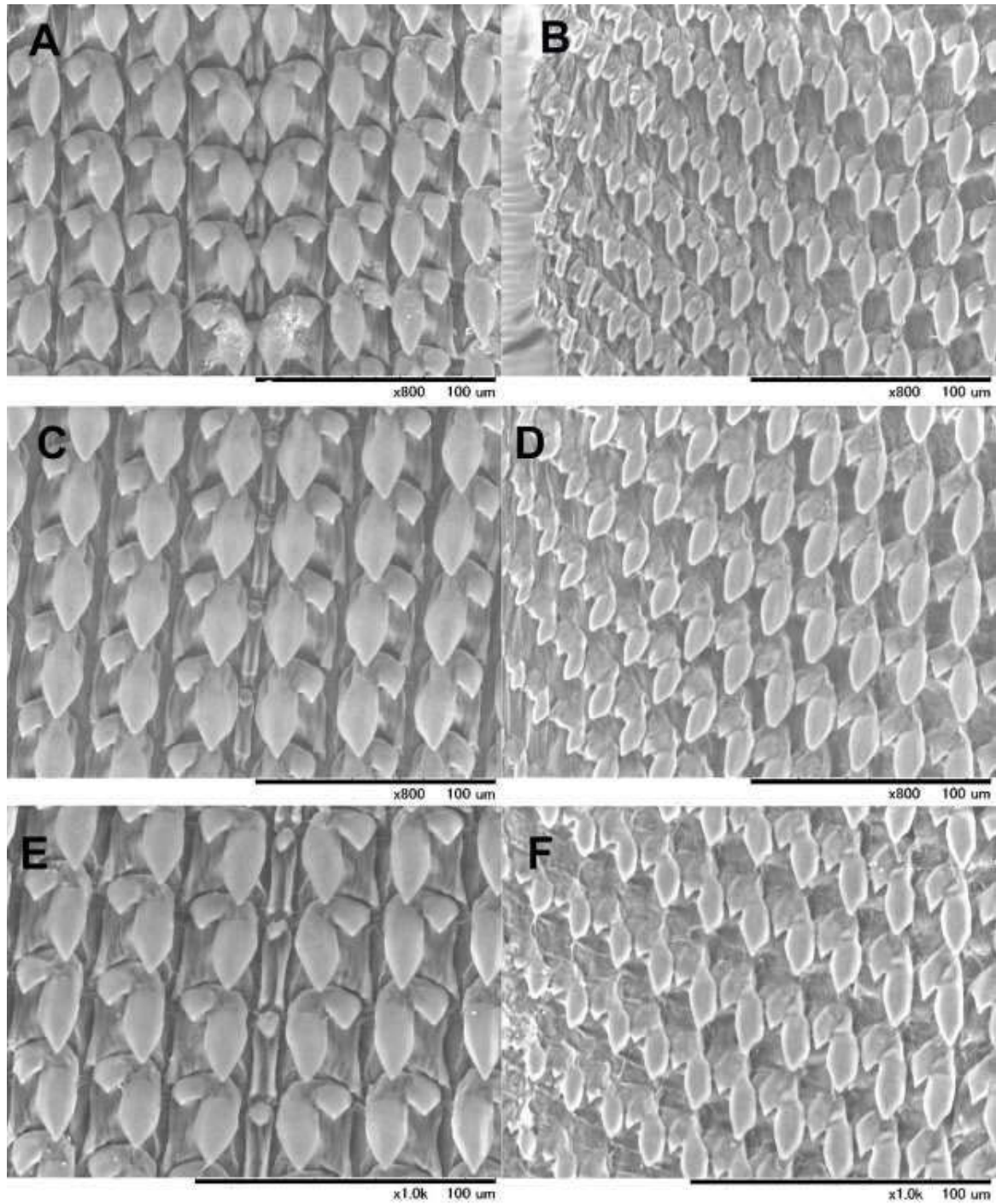


Figure 7.97. SEM images of radulae of Genus1 and *Plectopylis* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: Genus1 *dextrorsa*; C–D: *Plectopylis bensoni*; E–F: *Plectopylis species2*.

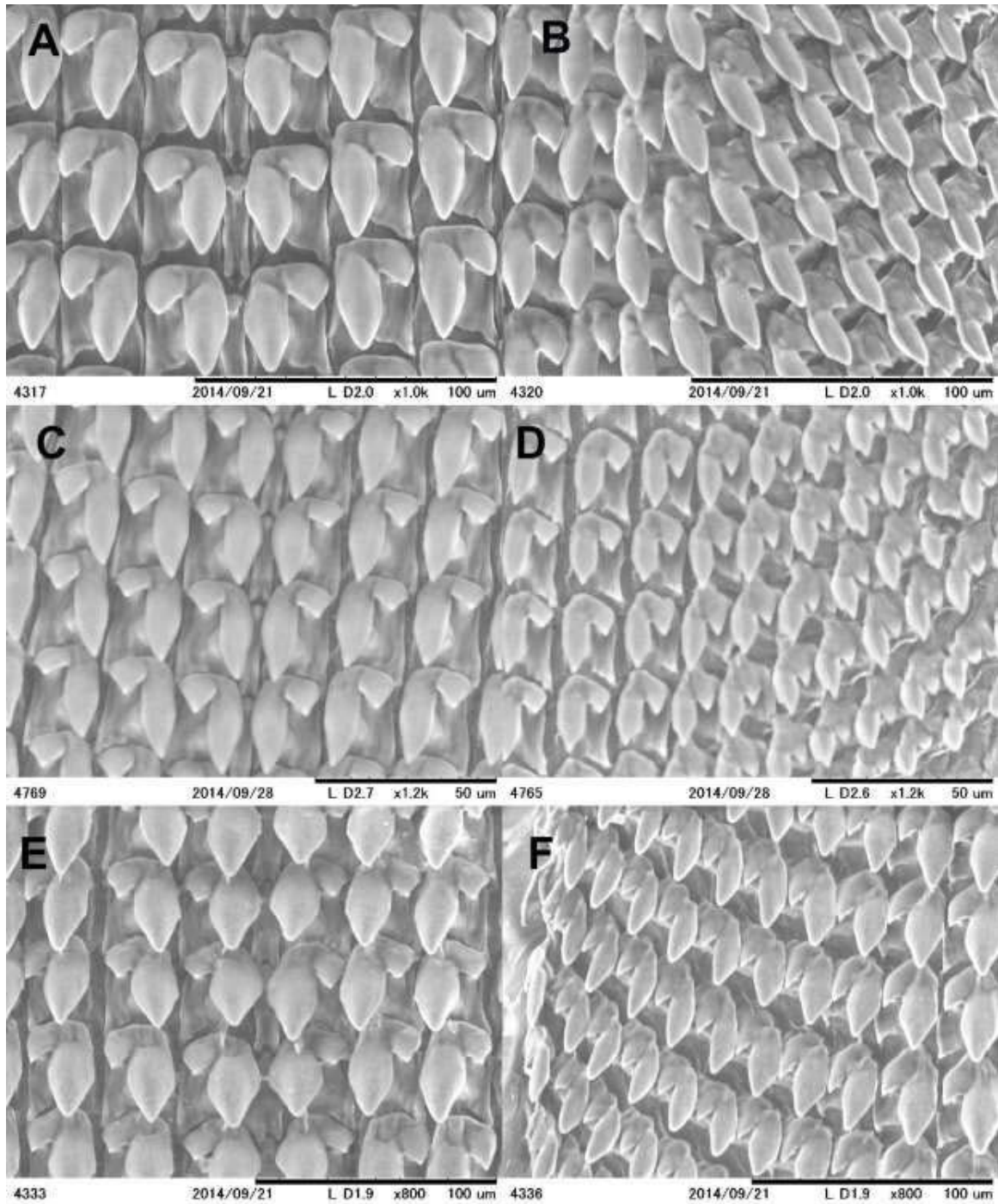


Figure 7.98. SEM images of radulae of *Chersaecia* and Genus3 species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *Chersaecia shanensis*; C–D: *Chersaecia perrierae*; E–F: Genus3 *laomontana*, 16L06.

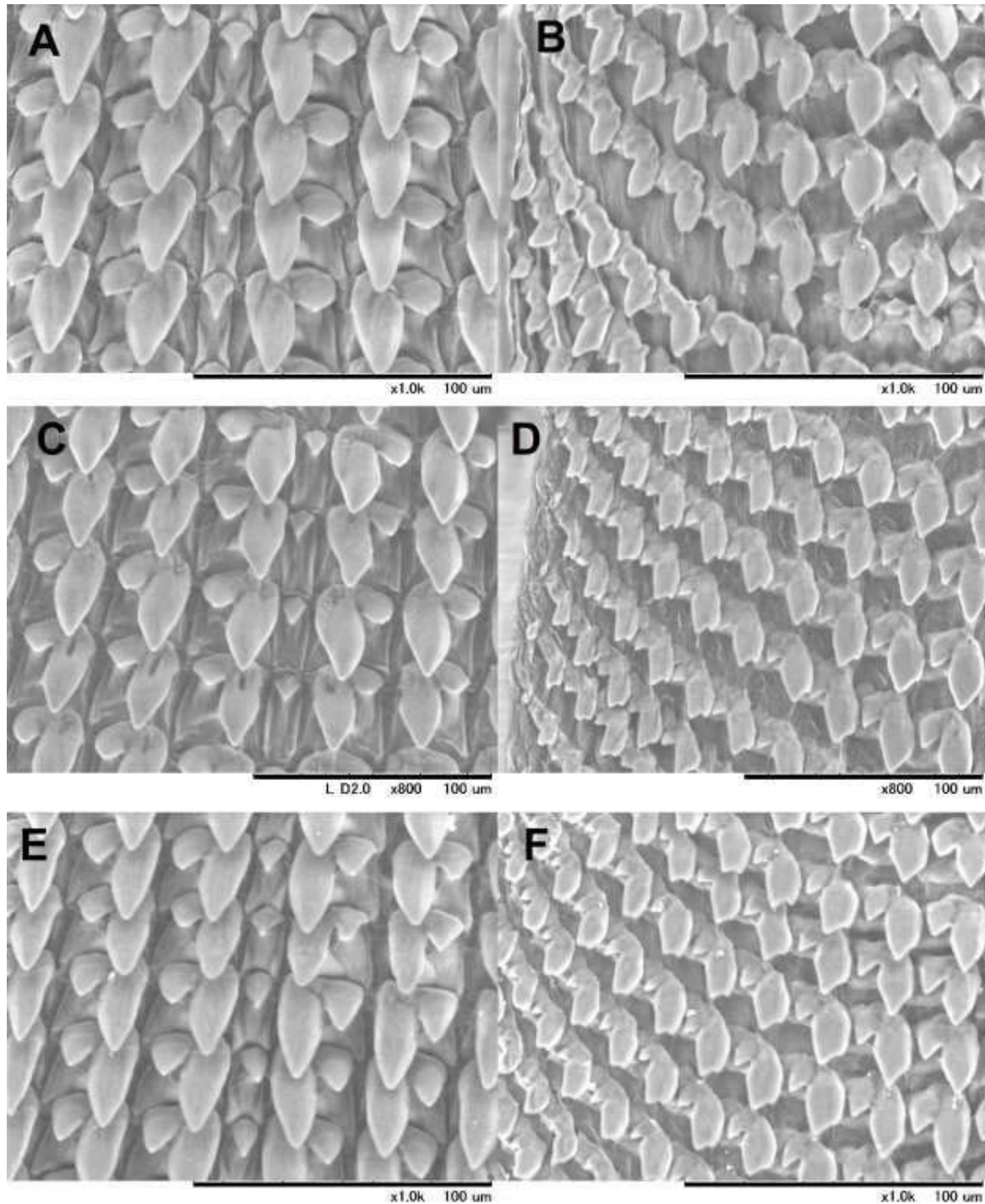


Figure 7.99. SEM images of radulae of *Gudeodiscus (Veludiscus)* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *Gudeodiscus (Veludiscus) emigrans otanii* Páll-Gergely & Hunyadi 2013, 20041113B; C–D: *G. (V.) eroessi eroessi* Páll-Gergely & Hunyadi 2013, 20041109B; E–F: *G. (V.) okuboi* Páll-Gergely & Hunyadi 2013, 20041109A.

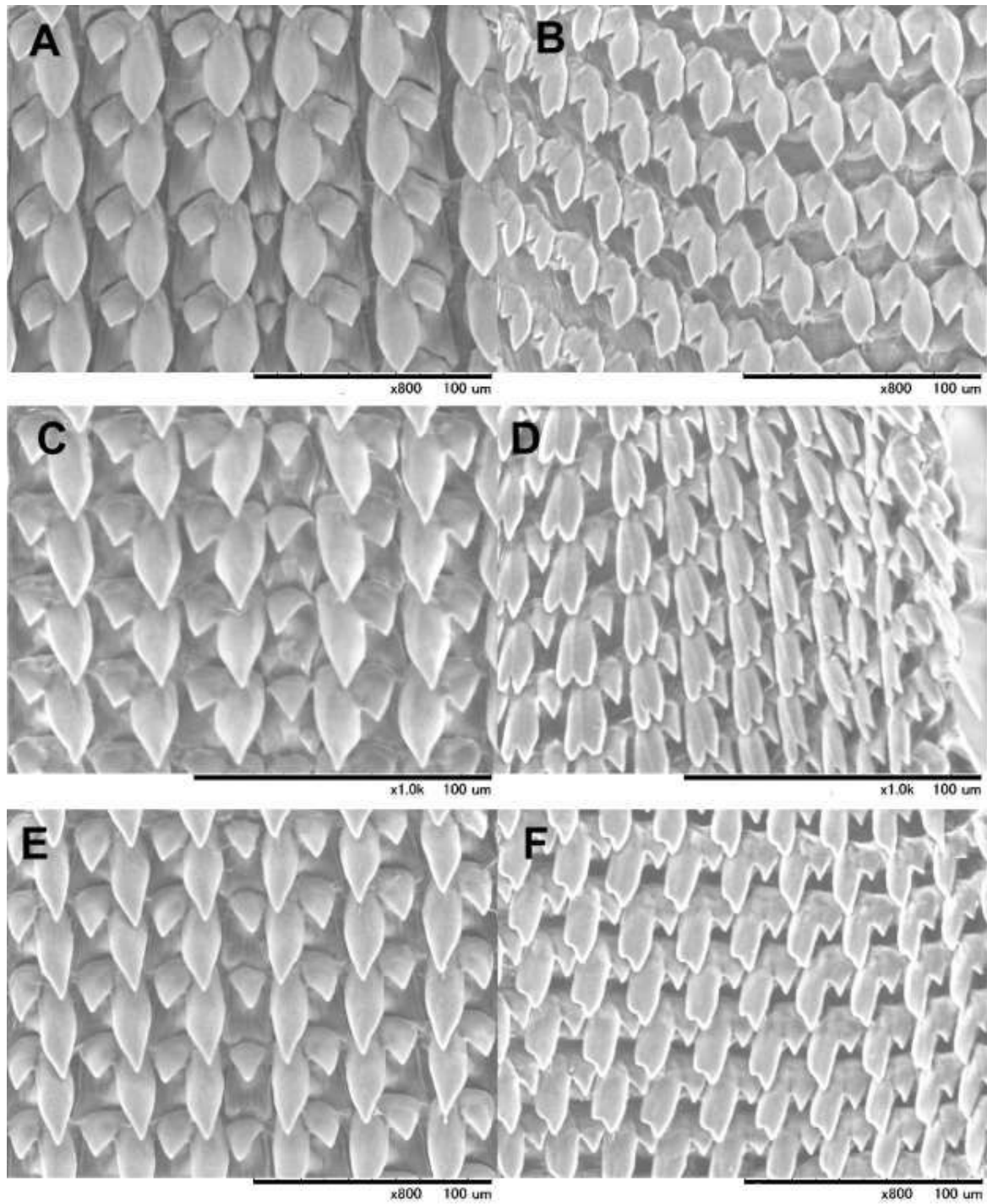


Figure 7.100. SEM images of radulae of *Gudeodiscus* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *G. (V.) pulvinaris pulvinaris* (Gould 1859), China, Hong Kong Peak, leg. Miu Yeung; C–D: *G. (G.) fischeri* (Gude 1901), Vn11-138; E–F: *Gudeodiscus (Gudeodiscus) giardi giardi* (Fischer 1898) 2011/87.

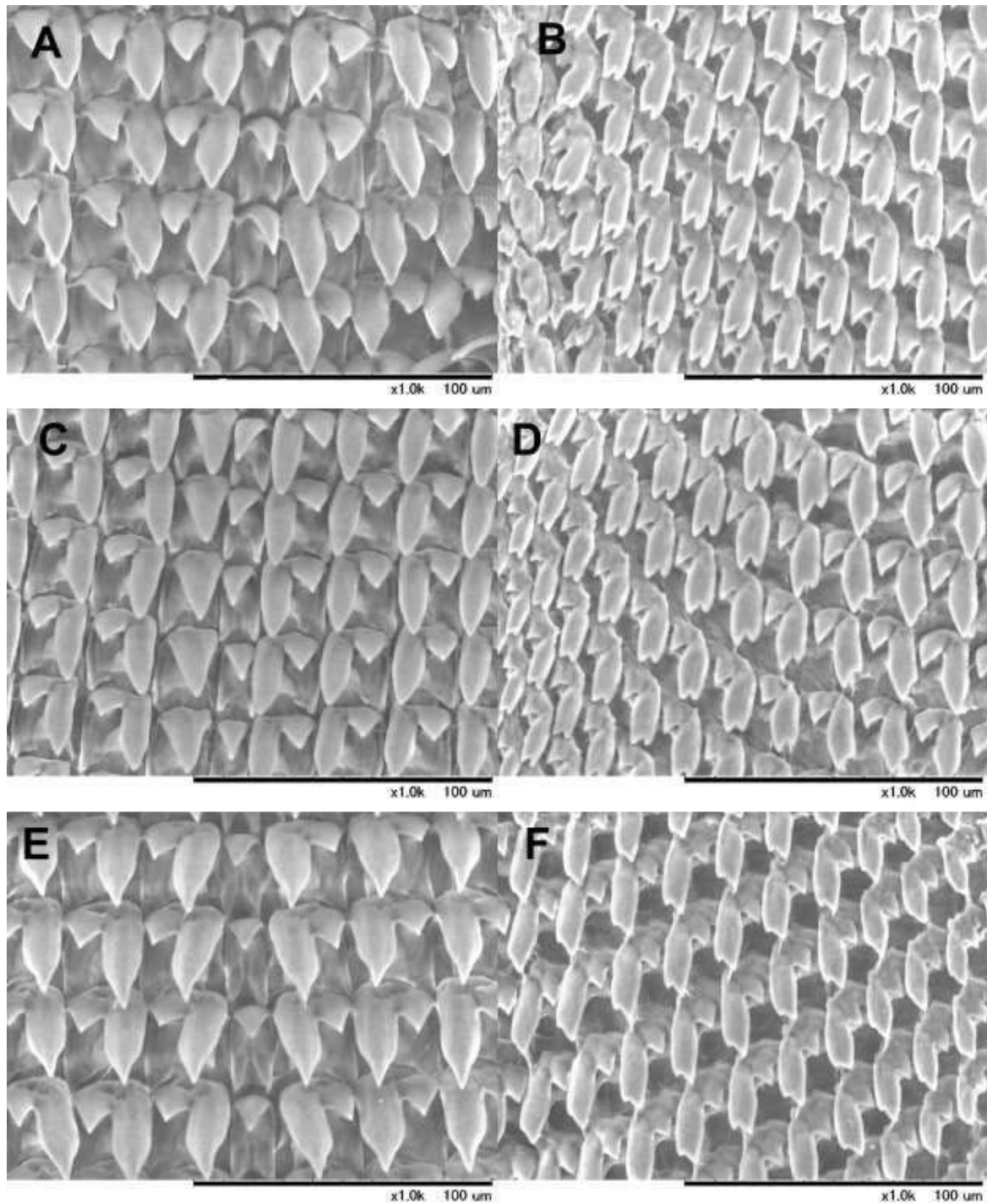


Figure 7.101. SEM images of radulae of *Gudeodiscus* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *G. (G.) messengeri raheemi* Páll-Gergely & Hunyadi u. ssp., Vn10-103; C–D: *G. (G.) multispira* (Möllendorff 1883), 20041112E; E–F: *G. (G.) phlyarius* (Mabille 1887), Vn11-157.

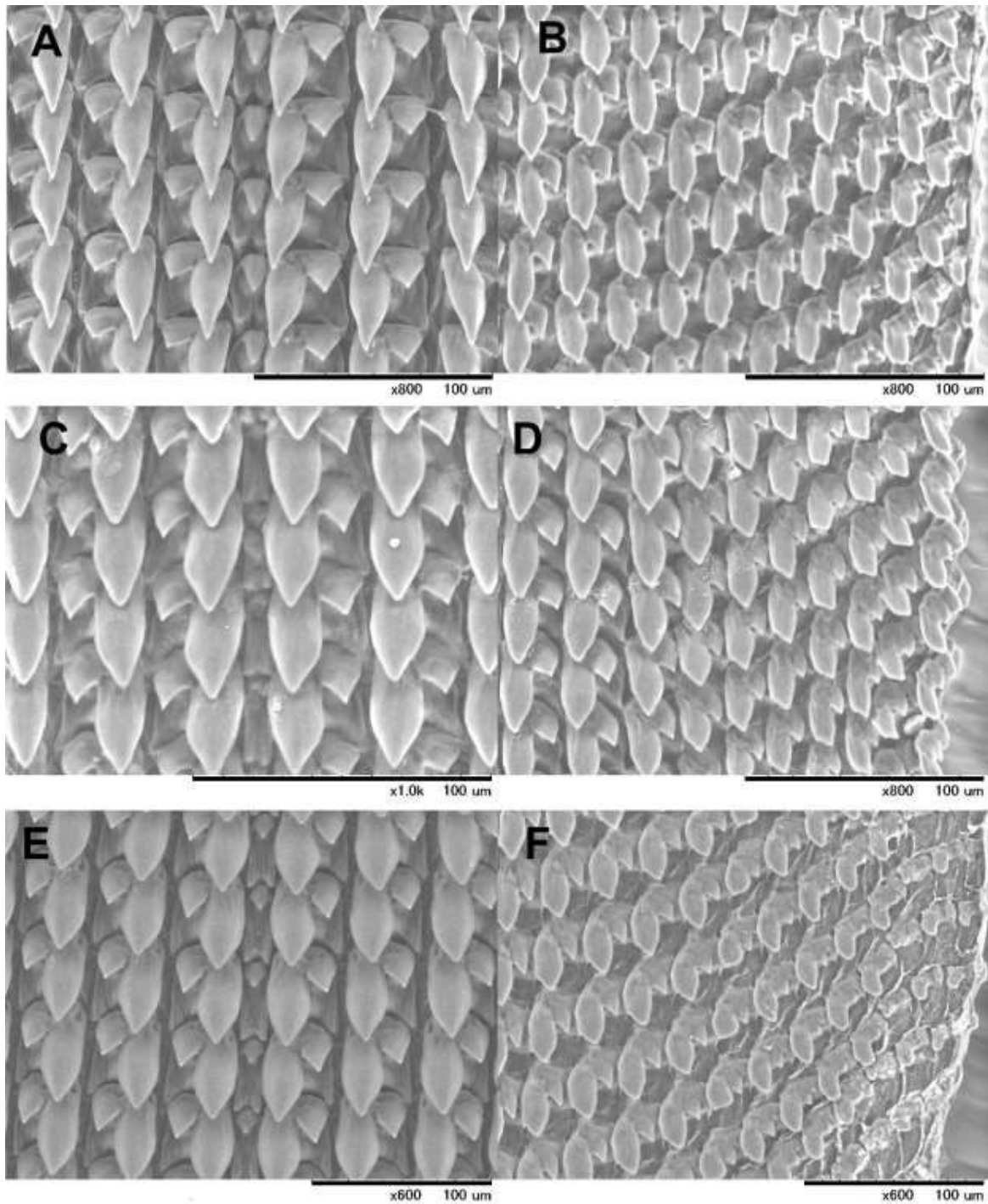


Figure 7.102. SEM images of radulae of *Gudeodiscus* and *Halongella* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *G. (G.) villedaryi* (Ancey 1888), 2011/102; C–D: *Halongella fruhstorferi* (Möllendorff 1901), Vn11-171; E–F: *Halongella schlumbergeri* (Morlet 1886), 20071122D.

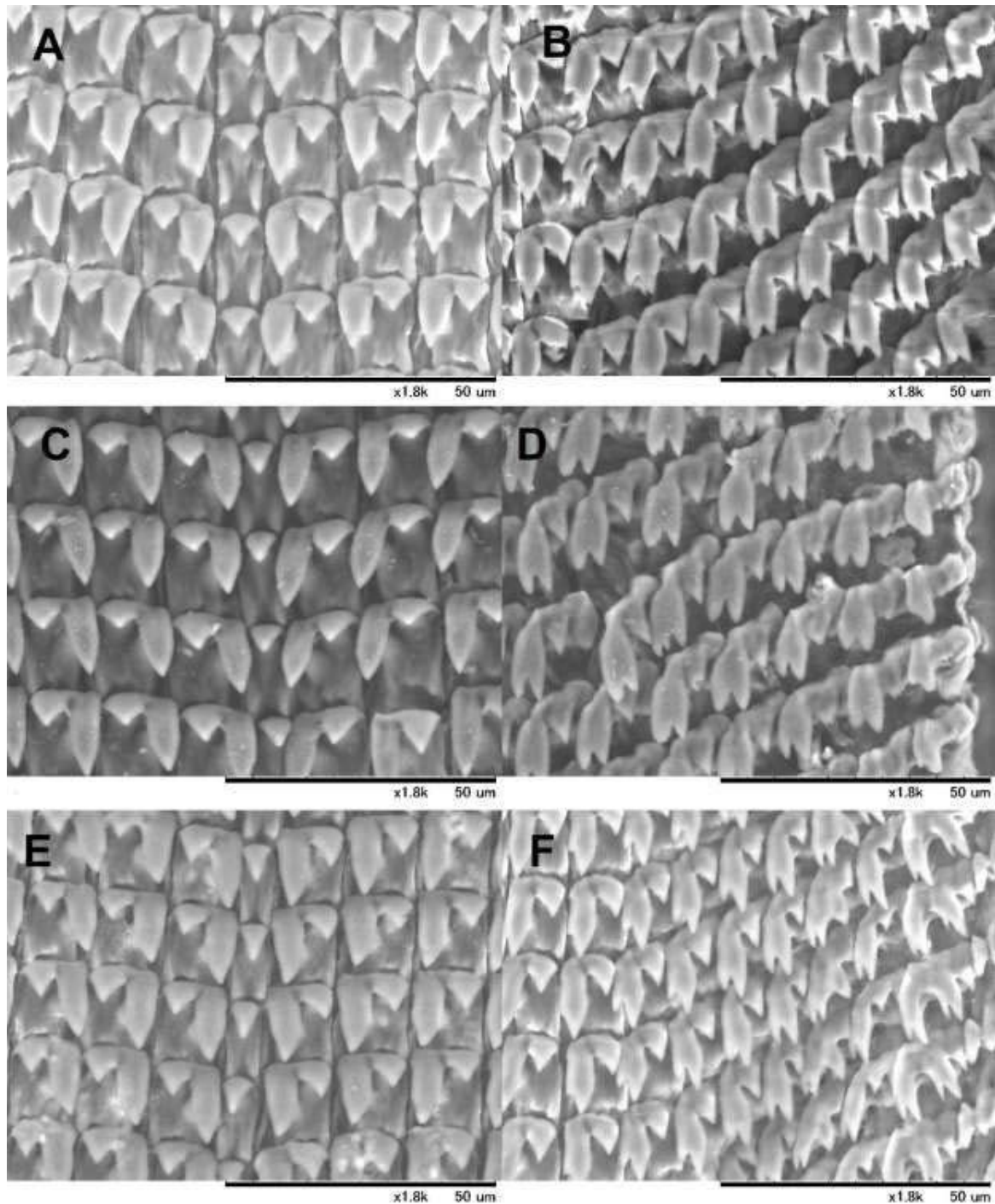


Figure 7.103. SEM images of radulae of *Sicradiscus* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *Sicradiscus invius* (Heude 1885), 20130917A; C–D: *S. mansuyi* (Gude 1908), 2012/44; E–F: *S. schistoptychia* (Möllendorff 1886), 2010/48.

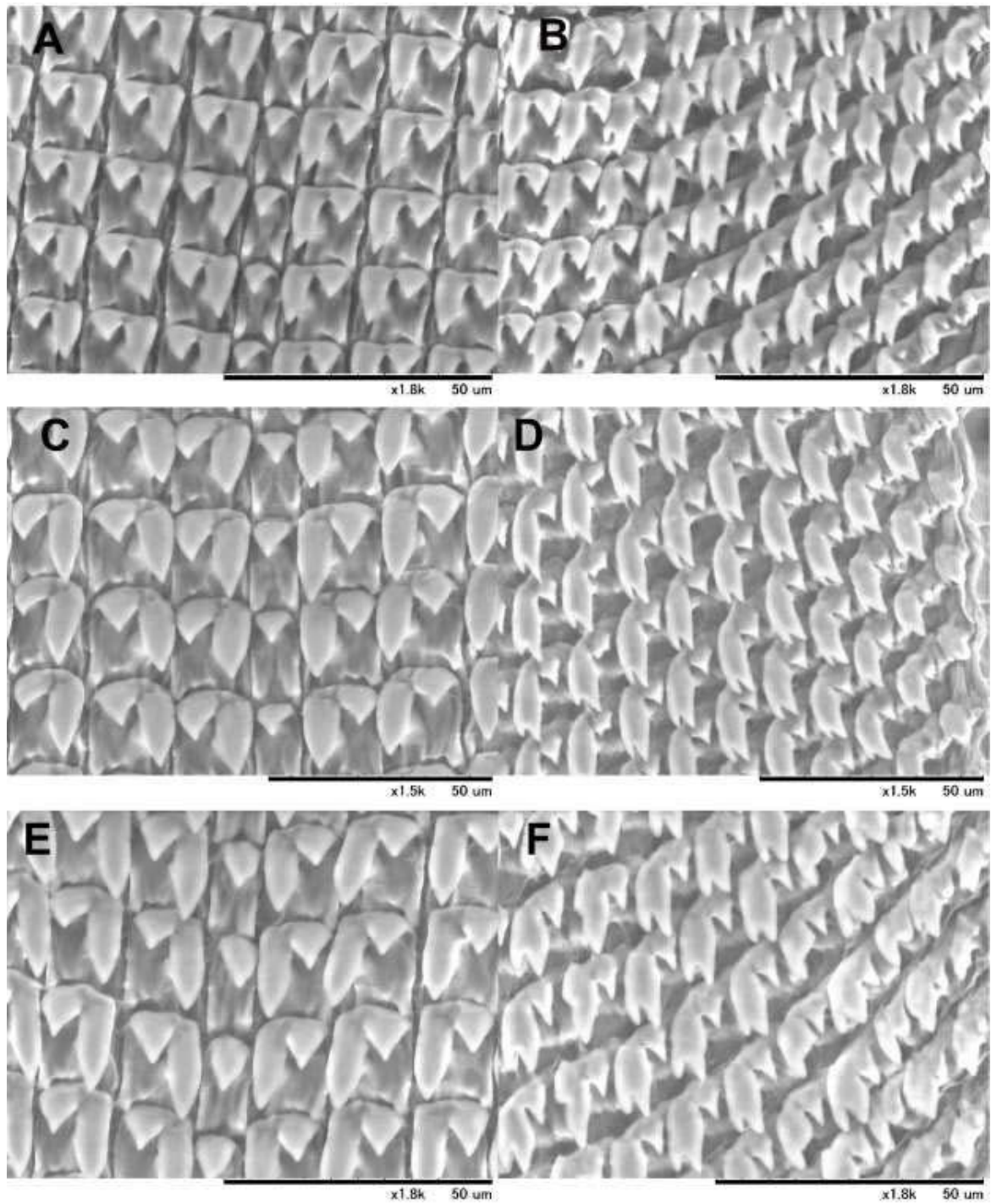


Figure 7.104. SEM images of radulae of *Sicradiscus* and *Sinicola* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *Sicradiscus transitus* Páll-Gergely 2013, 2013/8; C–D: *Sinicola asamiana* Páll-Gergely 2013, 20130916A; E–F: *S. emoriens* (Gredler 1881), 2010/41.

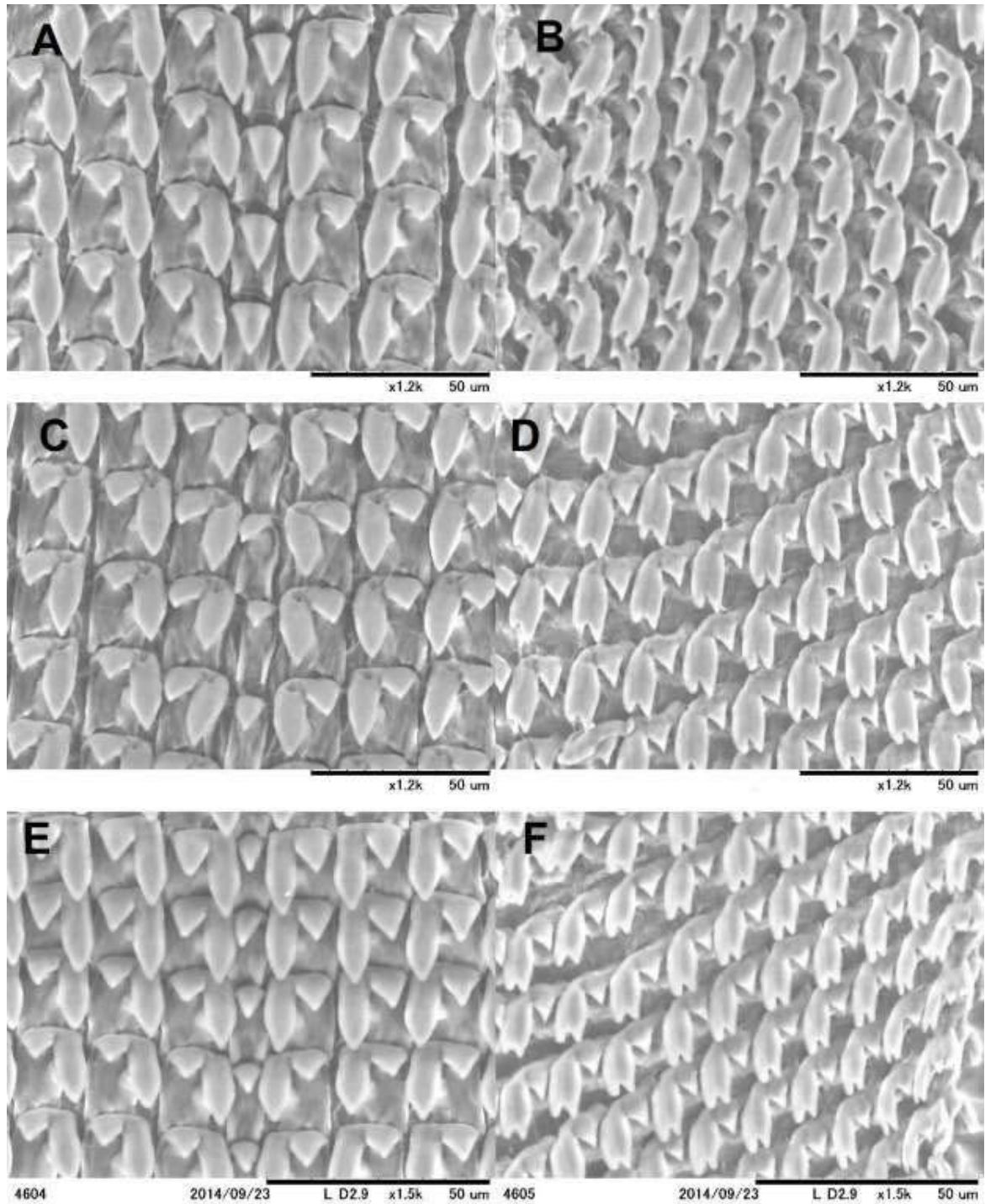


Figure 7.105. SEM images of radulae of *Sinicola* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *Sinicola fimbriosa* (von Martens 1875), 2010/3; C–D: *Sinicola jugatoria* (Ancey 1885), 2010/25; E–F: *Sinicola murata* (Heude 1885), 20130916A.

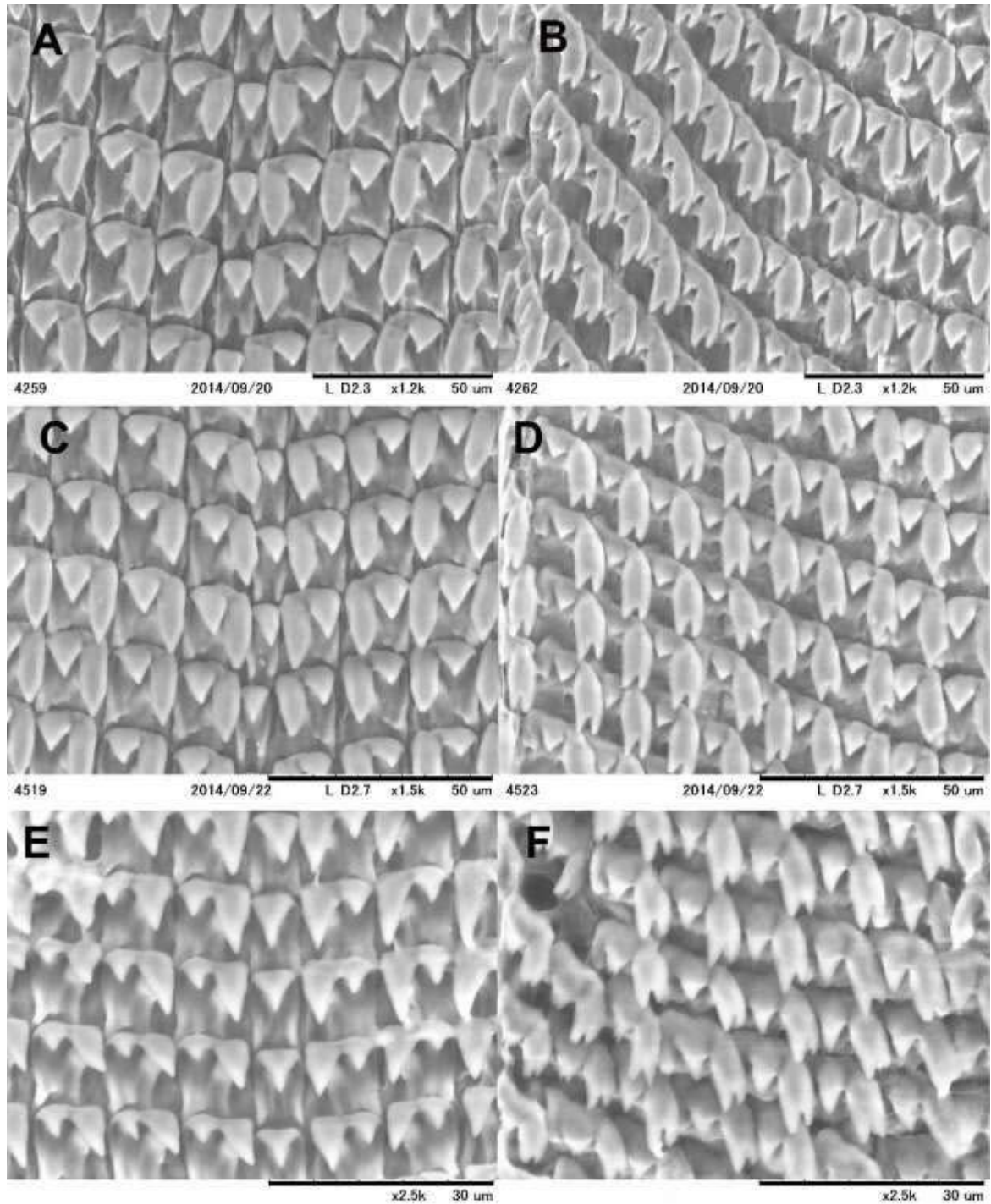


Figure 7.106. SEM images of radulae of *Sinicola* and *Endothyrella* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *S. reserata azona* (Gredler 1887), 20090308B; C–D: *S. stenochila* (Möllendorff 1885), 2010/30, E–F: *Endothyrella blanda* (Gude 1898), Silchar Cachar, F. Ede, coll. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.502.

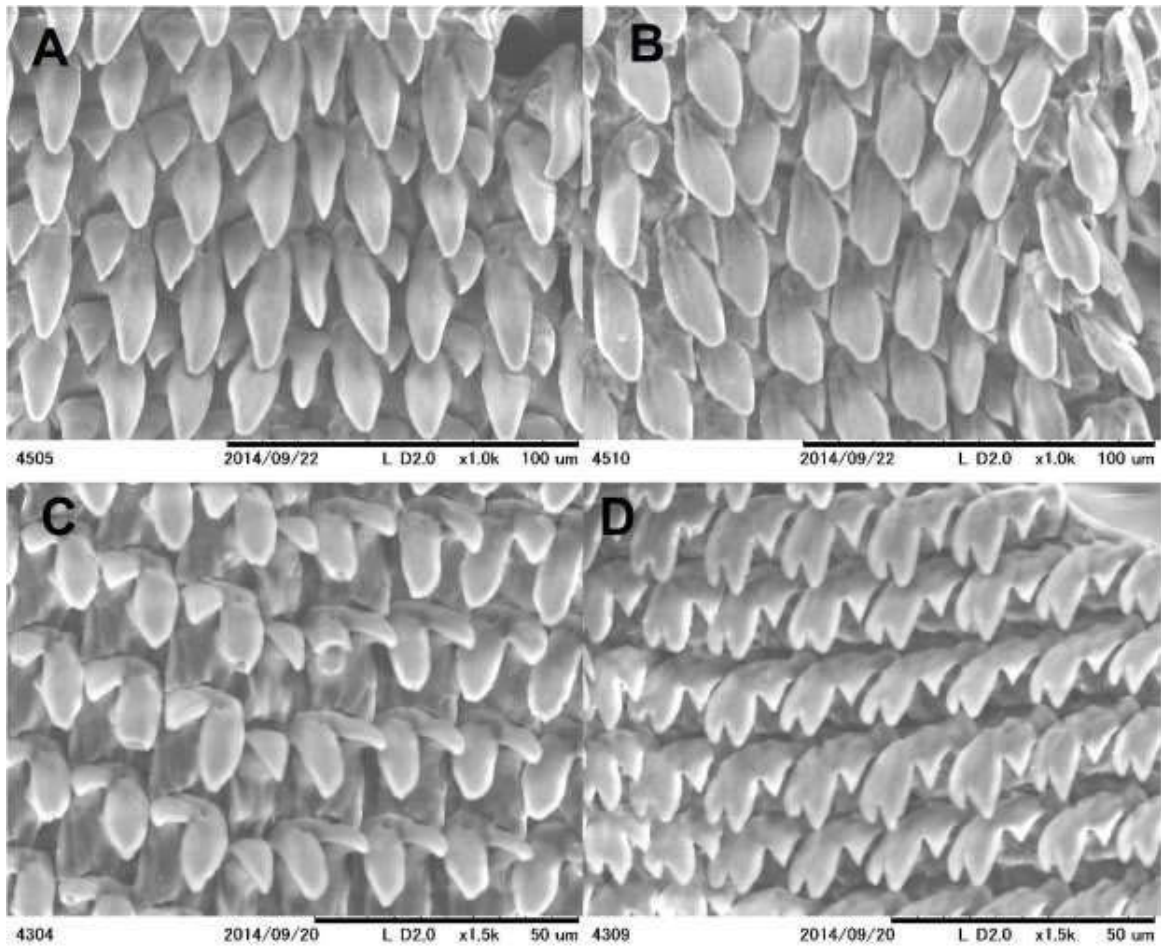


Figure 7.107. SEM images of radulae of *Endothyrella* species. Figures A, C, E show central tooth and the adjacent laterals, Figs B, D, F show the marginals. A–B: *Endothyrella fultoni* (Godwin-Austen 1892) Khasi, leg. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.598.; E–F: *Endothyrella plectostoma* (Benson 1836) Sikkim, leg. Godwin-Austen, Acc. no. 1830, NHMUK 1903.7.1.451.

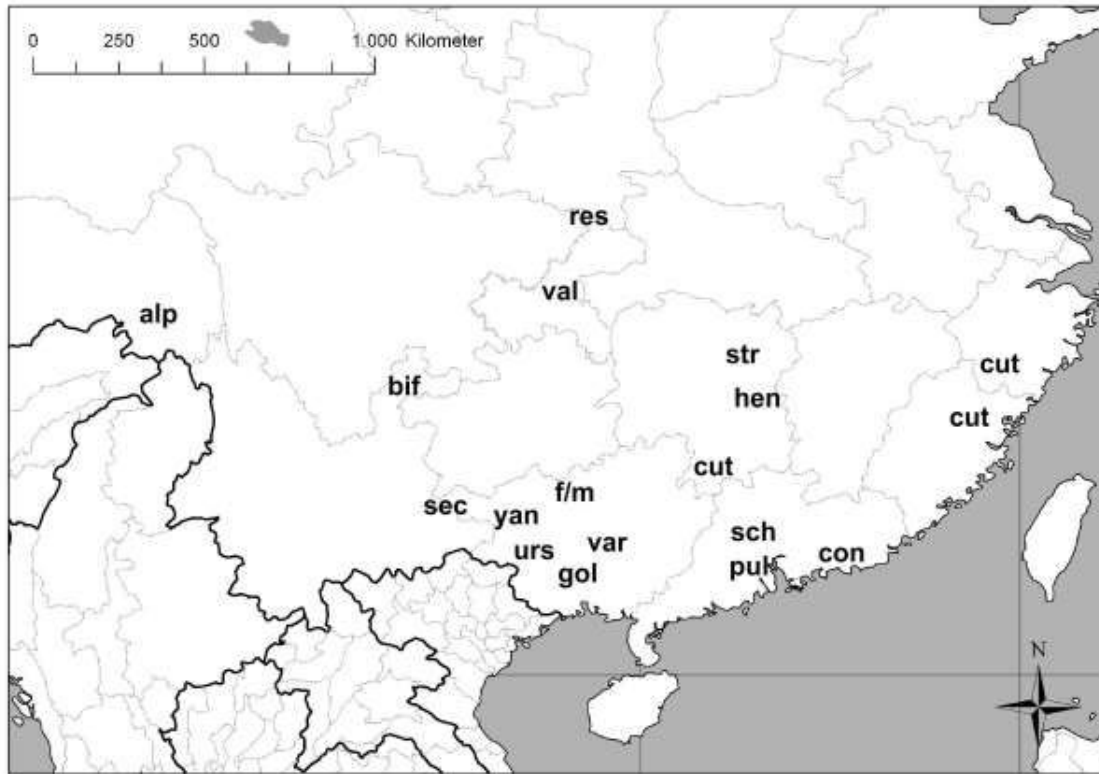


Figure 7.108. Approximate distribution of Chinese Plectopylidae species. Abbreviations: alp: *Sinicola alphonsi* (W. Blanford 1869), bif: *Sinicola biforis* (Heude 1885), con: type locality of *Plectopylis pulvinaris continentalis* Möllendorff 1885 (synonym of *Gudeodiscus pulvinaris pulvinaris* (Gould 1859)), cut: *Sicradiscus cutisculptus* (Möllendorff 1882), f/m: *Gudeodiscus eroessi fuscus* Páll-Gergely & Hunyadi 2013 and *Gudeodiscus marmoreus* Páll-Gergely 2014, gol: *Gudeodiscus goliath* Páll-Gergely & Hunyadi 2013, hen: *Sinicola reserata hensanensis* (Yen 1939), yan: *Gudeodiscus yanghaoi* Páll-Gergely & Hunyadi 2013, pul: *Gudeodiscus pulvinaris* (Gould 1859), res: *Sinicola reserata* (Heude 1885), sch: *Sinicola schmackeri* Páll-Gergely 2013, sec: *Sicradiscus securus* (Heude 1889), str: *Sinicola straeleni* (Yen 1937), urs: *Gudeodiscus ursula* Páll-Gergely & Hunyadi 2013, val: *Sinicola vallata* Heude 1889, var: *Sinicola vargabalinti* Páll-Gergely 2014. The locality of *Sin. alphonsi* and the occurrence of *Sic. cutisculpta* in Hunan may be probably wrong.

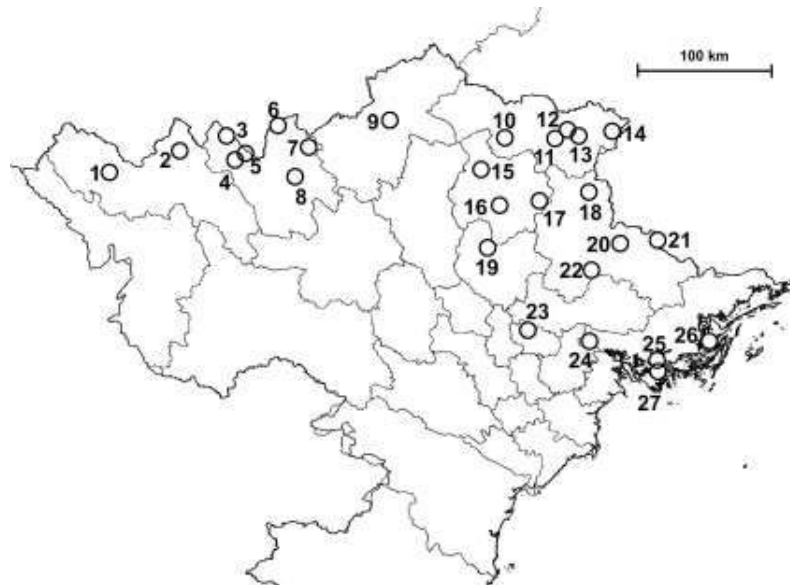


Figure 7.109. Locations mentioned in literature on plectopylid taxonomy. 1: Muong-Bo, 2: Phony-Tho, 3: Trinh-Thuong, 4: Muong-Hum, 5: Nat-Son (Nhat Son), 6: Muong-Kong, 7: Long-Ping, 8: Pac-Kha, 9: Ha-Giang, 10: Tinh-Tuc, 11: Cao-Bang, 12: Déo-Ma-Phuc, 13: Quang-Huyen, 14: Ha-Lang, 15: Cho-Ra, 16: Bac-Khan, 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.

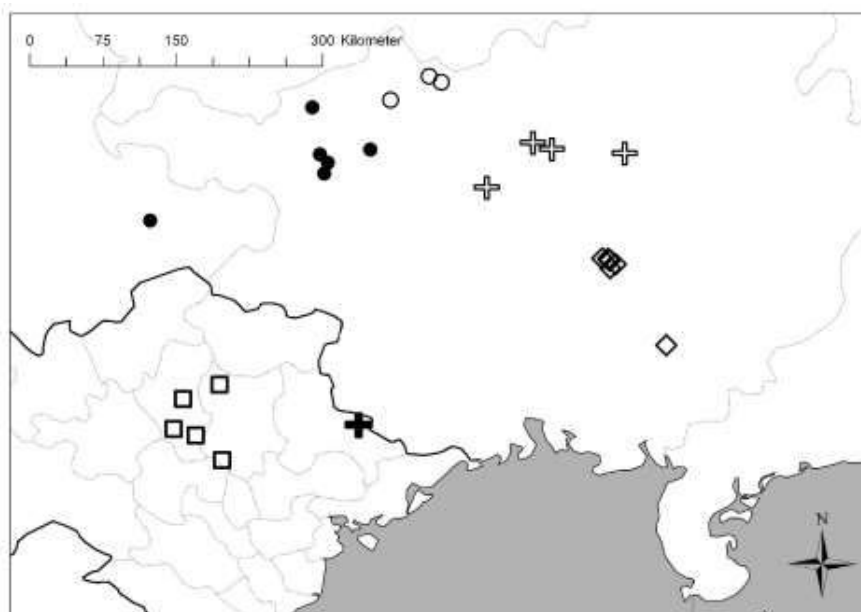


Figure 7.110. Distribution of *Gudeodiscus* Páll-Gergely 2013 and *Sicradiscus* Páll-Gergely 2013 species. Legends: filled circle: *Sicradiscus feheri* Páll-Gergely & Hunyadi 2013, empty circle: *Sicradiscus transitus* Páll-Gergely 2013, empty rhomb: *Gudeodiscus okuboi* Páll-Gergely & Hunyadi 2013, empty cross: *Gudeodiscus emigrans otanii* Páll-Gergely 2013, filled cross: approximate locality of *Gudeodiscus emigrans* (Möllendorff 1901), empty square: *Gudeodiscus emigrans quadrilamellatus* Páll-Gergely 2013.

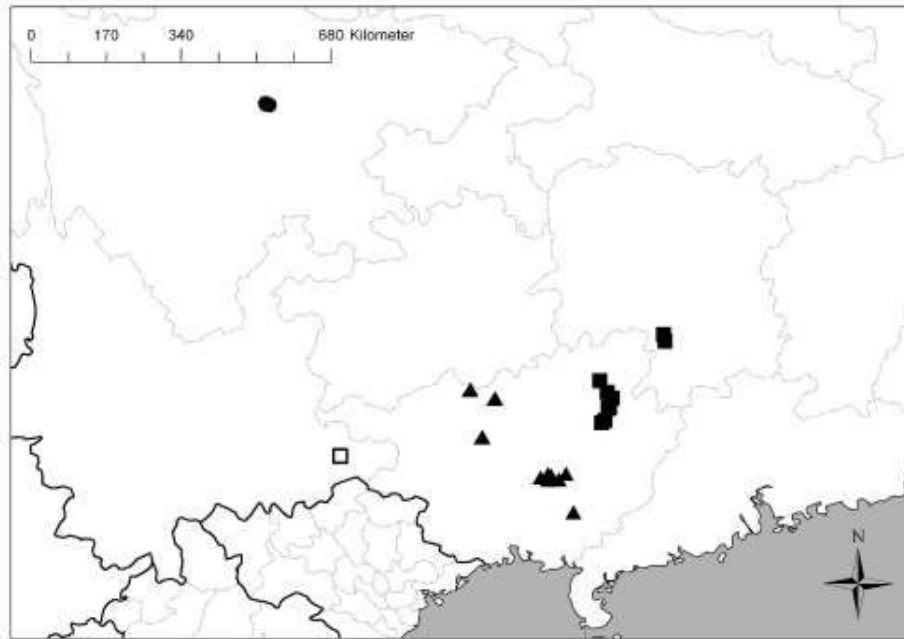


Figure 7.111. Distribution of *Gudeodiscus* Páll-Gergely 2013 and *Sicradiscus* Páll-Gergely 2013 species. Legends: circle: *Sicradiscus invius* (Heude 1885), empty square: *Gudeodiscus yunnanensis* Páll-Gergely 2013, filled square: *Gudeodiscus multispira* (Möllendorff 1883), triangle: *Gudeodiscus pulvinaris robustus* Páll-Gergely & Hunyadi 2013

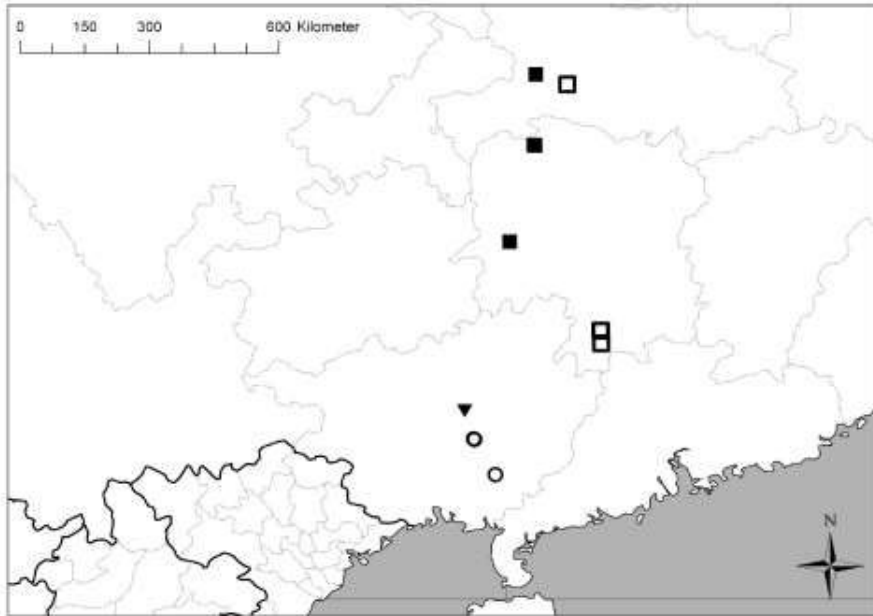


Figure 7.112. Distribution of *Gudeodiscus* Páll-Gergely 2013 and *Sicradiscus* Páll-Gergely 2013 species. Legends: circle: *Gudeodiscus eroessi* Páll-Gergely & Hunyadi 2013, empty square: *Sicradiscus schistoptychia* (Möllendorff 1886), filled square: *Sicradiscus diptychia* (Möllendorff 1885); filled triangle, top down: *Gudeodiscus eroessi hemisculptus* Páll-Gergely 2013.

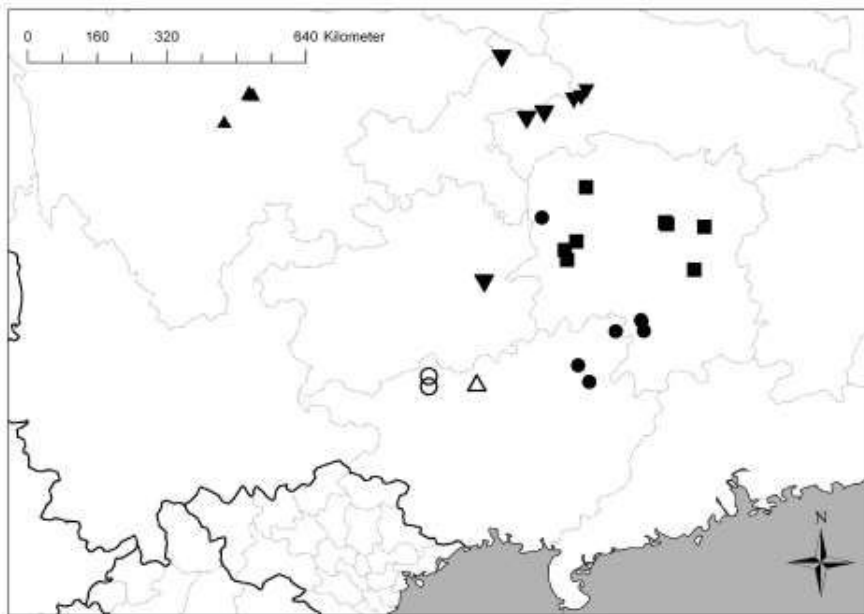


Figure 7.113. Distribution of *Sinicola* Gude 1899 and *Gudeodiscus* Páll-Gergely 2013 species. Legends: filled triangle, top down: *Sinicola stenochila* (Möllendorff 1885), filled triangle, top up: *Sinicola murata* (Heude 1885), square: *Sinicola fimbriosa* (von Martens 1875), circle: *Sinicola emoriens* (Gredler 1881), empty circle: *Gudeodiscus soosi* Páll-Gergely 2013, empty triangle, top up: *Gudeodiscus concavus* Páll-Gergely 2013.

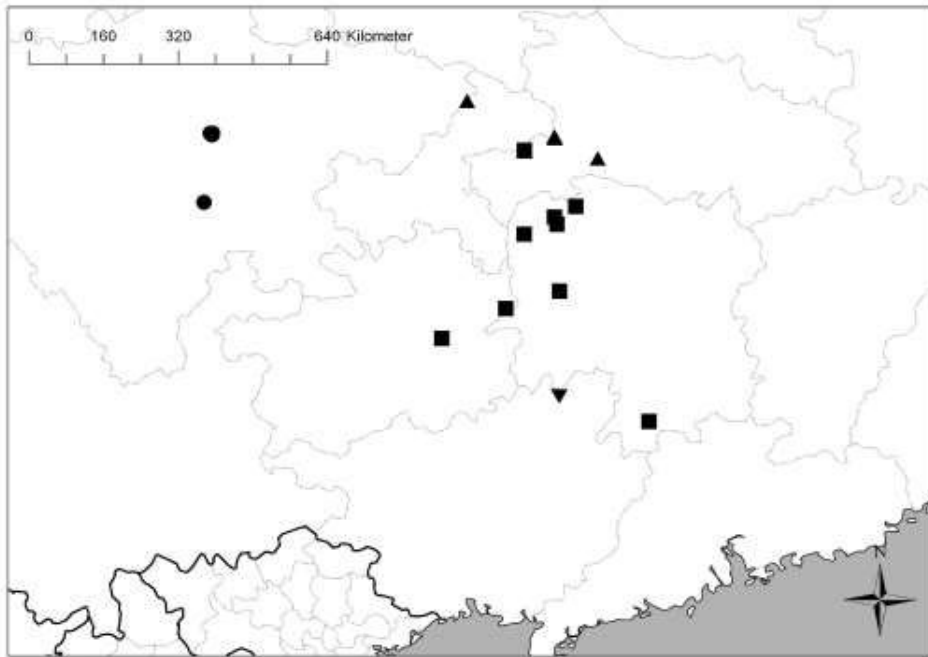


Figure 7.114. Distribution of *Sinicola* Gude 1899 species. Legends: triangle, top down: *Sinicola stenomphala* Páll-Gergely & Hunyadi 2013, triangle, top up: *Sinicola jugatoria* (Ancey 1885), square: *Sinicola reserata azona* (Gredler 1887), circle: *Sinicola asamiana* Páll-Gergely 2013.

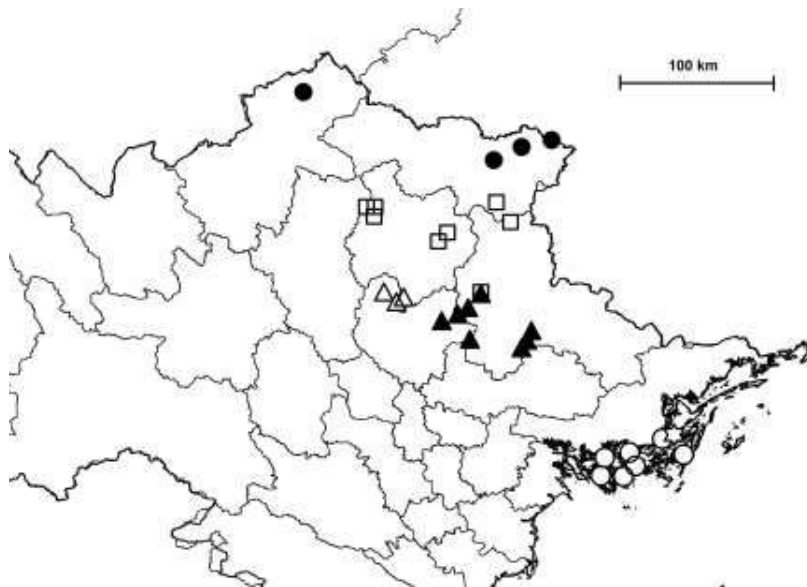


Figure 7.115. Distribution of *Gudeodiscus*, *Halongella* and *Sicradiscus* species. Legends: empty circle: *Halongella schlumbergeri* (Morelet 1886), star (close to the circles): *H. fruhstorferi* (Möllendorff 1901), empty triangle: *Gudeodiscus (Gudeodiscus) dautzenbergi* (Gude 1901), filled triangle *G. (G.) villedaryi* (Ancey 1888), empty square: *G. (G.) anceyi* (Gude 1901), filled circle: *Sicradiscus mansuyi* (Gude 1908).

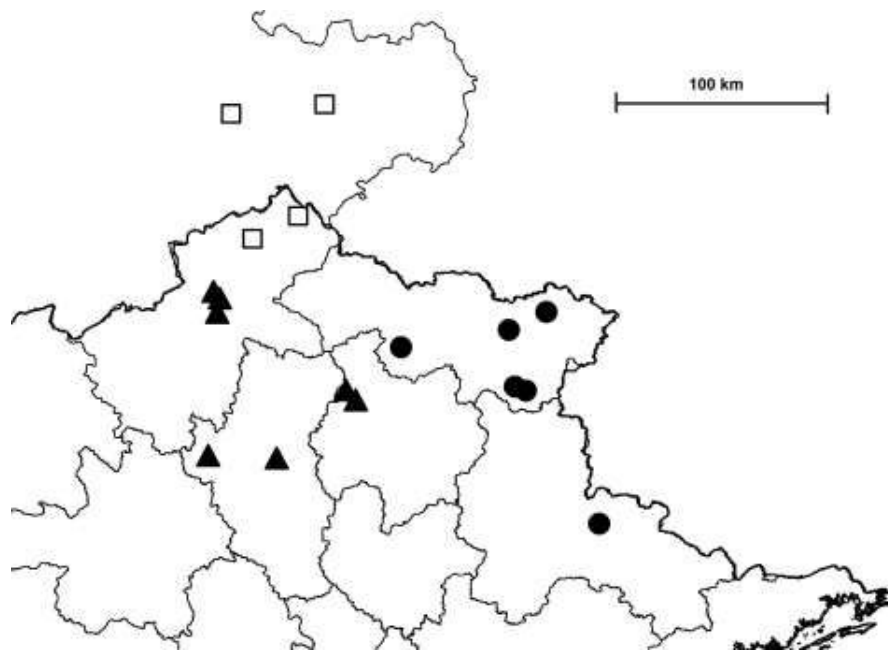


Figure 7.116. Distribution of *Gudeodiscus* species. Legends: filled circle: *Gudeodiscus* (*Gudeodiscus*?) *suprafilaris* (Gude 1908), triangle: *G. (G.) fischeri* (Gude 1901), empty square: *G. (G.) cyrtochilus* (Gude 1909).

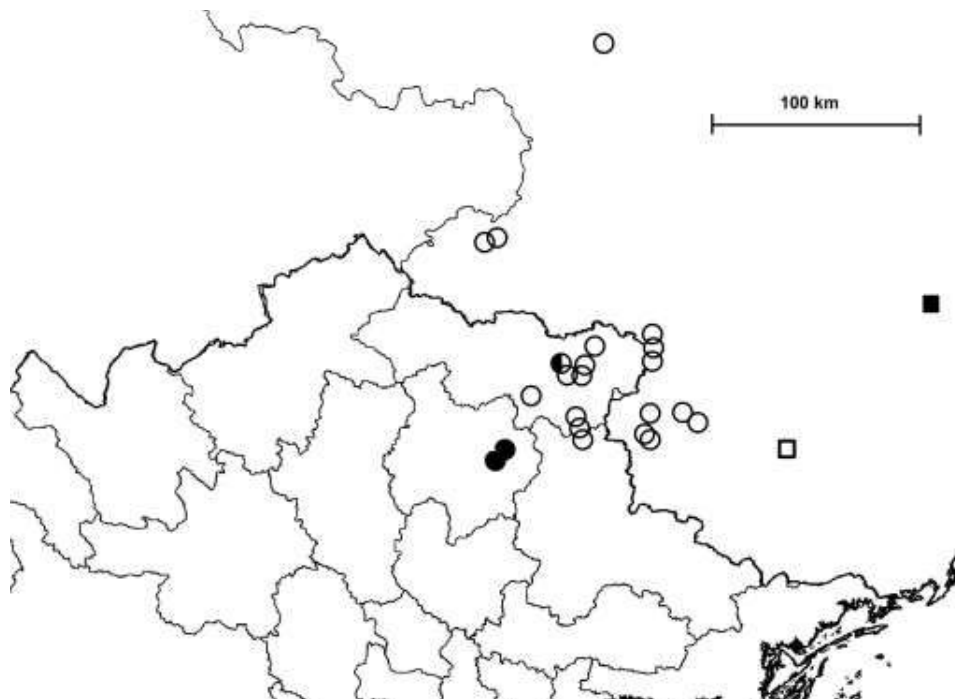


Figure 7.117. Distribution of *Gudeodiscus* species. Legends: empty circle: *G. (G.) giardi giardi* (Fischer 1898), filled square: *Gudeodiscus giardi oharai* Páll-Gergely 2013, empty square: *Gudeodiscus giardi szekeresi* Páll-Gergely & Hunyadi 2013; filled circle: *G. (G.) francoisi* (Fischer 1899), semi filled circle: co-occurrence of the latter two species.

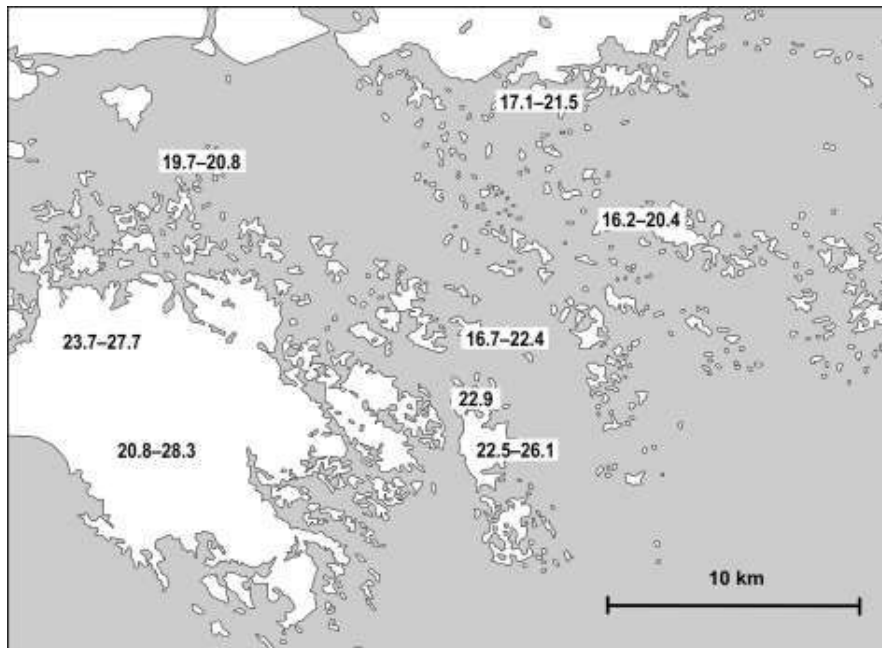


Figure 7.118. Shell widths of *Halongella schlumbergeri* (mm) in the Halong Bay Area.

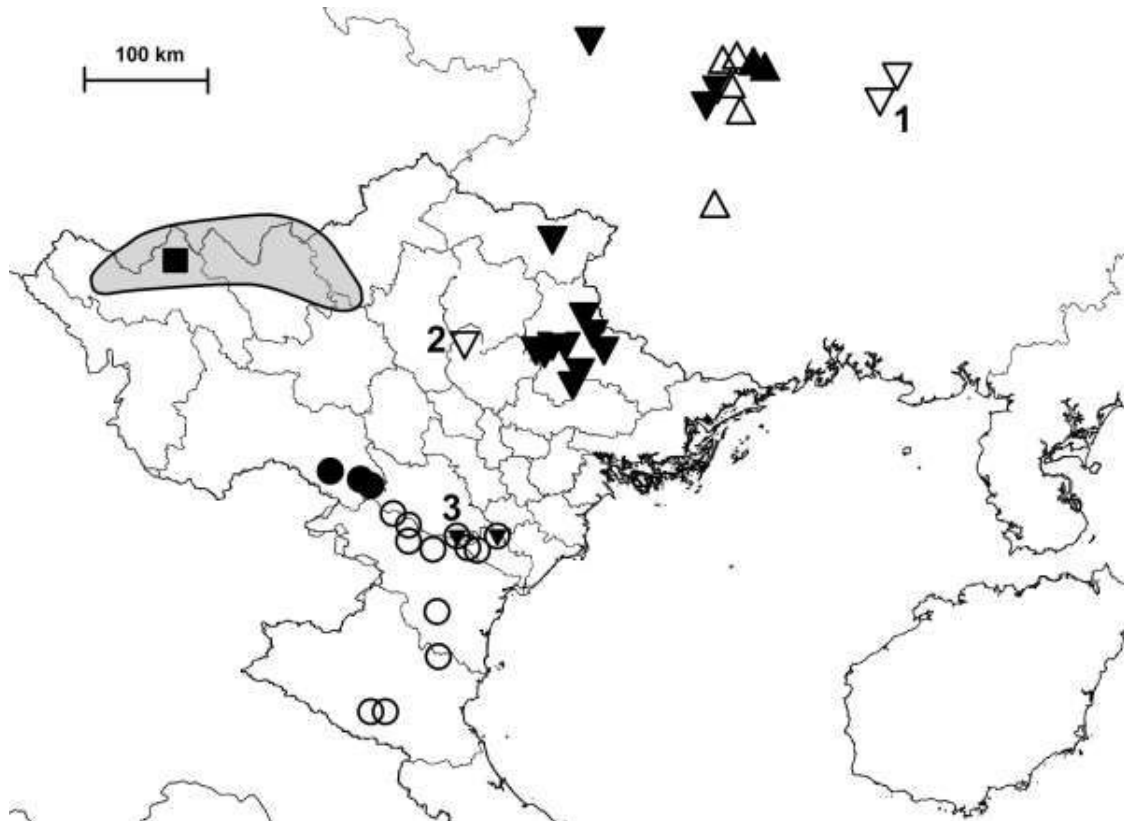


Figure 7.119. Distribution of *Gudeodiscus* Páll-Gergely 2013 species. Legends: filled triangle, top down: typical *Gudeodiscus (Gudeodiscus) phlyarius* (Mabille 1887), filled triangle, top up: "*Gudeodiscus phlyarius weneri* Páll-Gergely 2013" (synonym of *phlyarius*); empty triangle, top up: *G. (G.) phlyarius* populations showing transitional characters towards *weneri* in terms of shell shape; empty triangle, top up: atypical *G. (G.) phlyarius*; empty circle: *Gudeodiscus messengeri raheemi* u. ssp., filled circle: *G. (G.?) hemmeni* u. sp. (in all localities it co-occurs with *G. (G.) messengeri raheemi* u. ssp.); circle with filled triangle in the middle: co-occurrence of *G. (G.) messengeri raheemi* u. ssp. and atypical *G. (G.) phlyarius*. The shaded area indicates the area inhabited by *G. (G.) messengeri messengeri* (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.

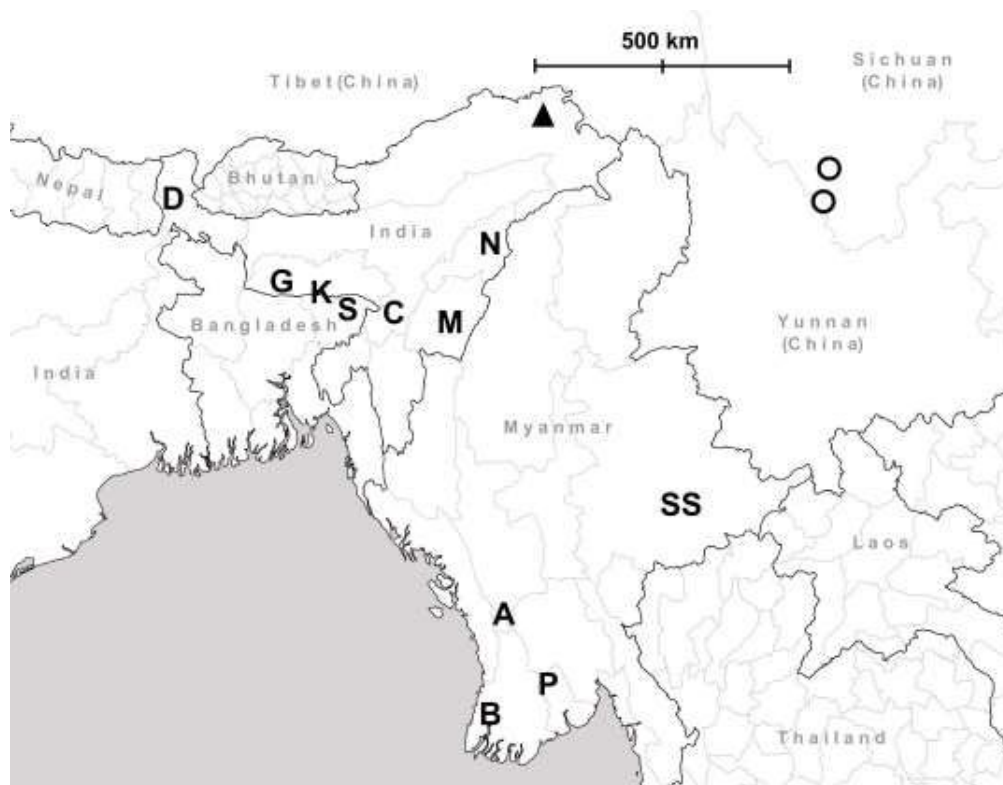


Figure 7.120. Empty circle: *Endothyrella* species 6 u. sp.; Filled triangle, top up: type locality of *Endothyrella babbagei*. Letter indicate localities of *Endothyrella plectostoma* (Benson 1836). Abbreviations: A: Arakan Hills, B: Bassein (Pathein), C: Silchar (Cachar), D: Darjeeling, G: Garo Hills, K: Khasi Hills, M: Manipur, N: Naga Hills, P: Pegu (Bago), S: Sylhet, SS: Southern Shan-States.

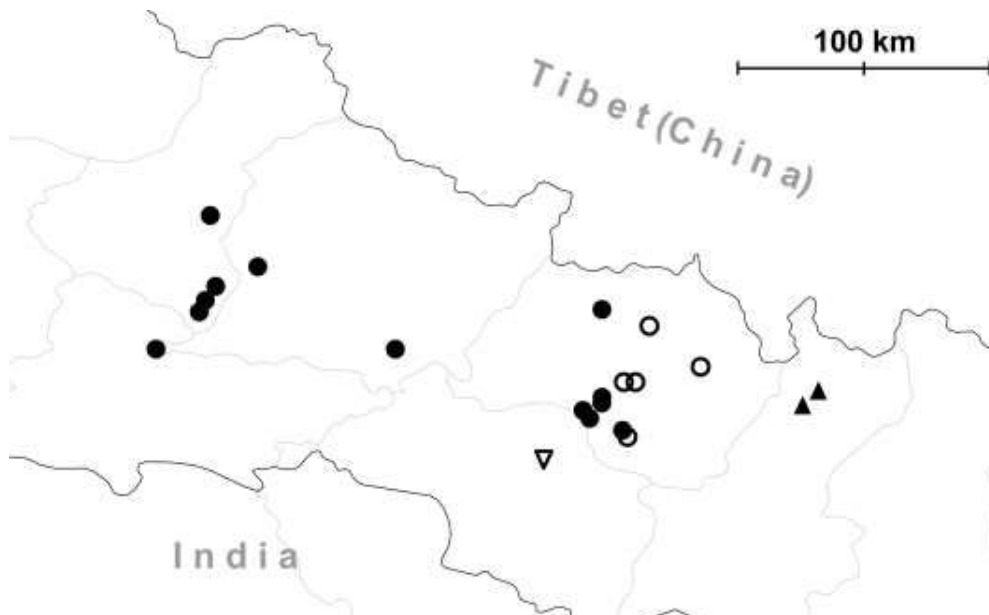


Figure 7.121. Distribution of *Endothyrella* species in Nepal. Filled circle: *Endothyrella* species8 n. sp; filled triangle, top up: *Endothyrella* species5 u. sp.; empty triangle, top down: *Endothyrella* species4 u. sp.; empty circle: *Endothyrella* nomen novum1 nom nov.

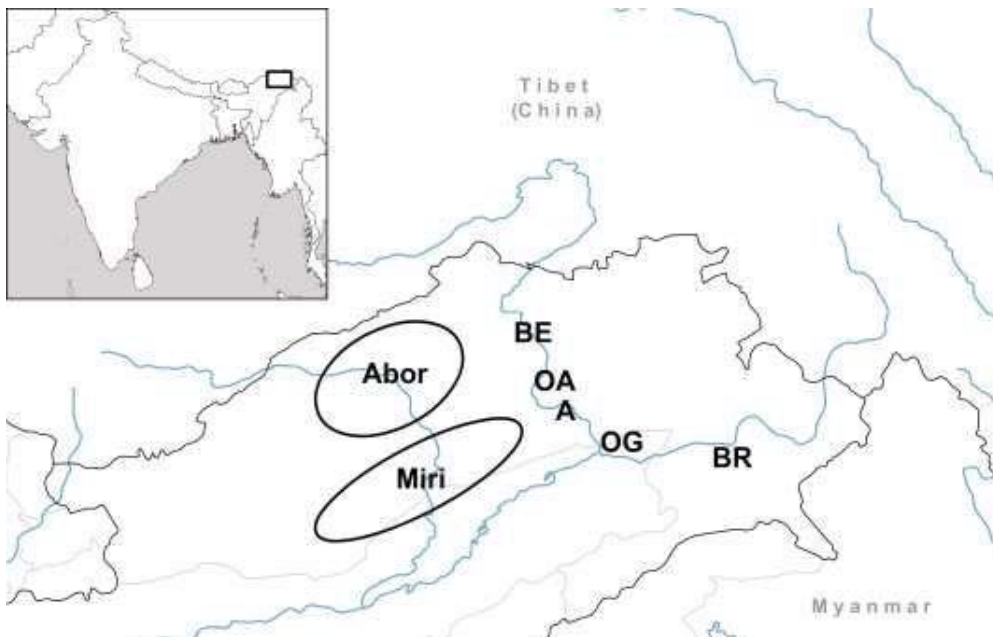


Figure 7.122. Distribution of *Endothyrella* species in Northeast India. Abbreviations: A: type locality of *Endothyrella aborensis* (Gude 1915); Abor: Abor Hills (type locality of *Endothyrella williamsoni* (Gude 1915), BE: type locality of *Endothyrella bedfordi* (Gude 1915); BR: Type locality of *Endothyrella brahma* (Godwin-Austen 1879); Miri: Miri Hills (type locality of *Endothyrella miriensis* (Gude 1915); OA: Type locality of *Endothyrella oakesi* (Gude 1915); OG: Type locality of *Endothyrella oglei* (Godwin-Austen 1879).

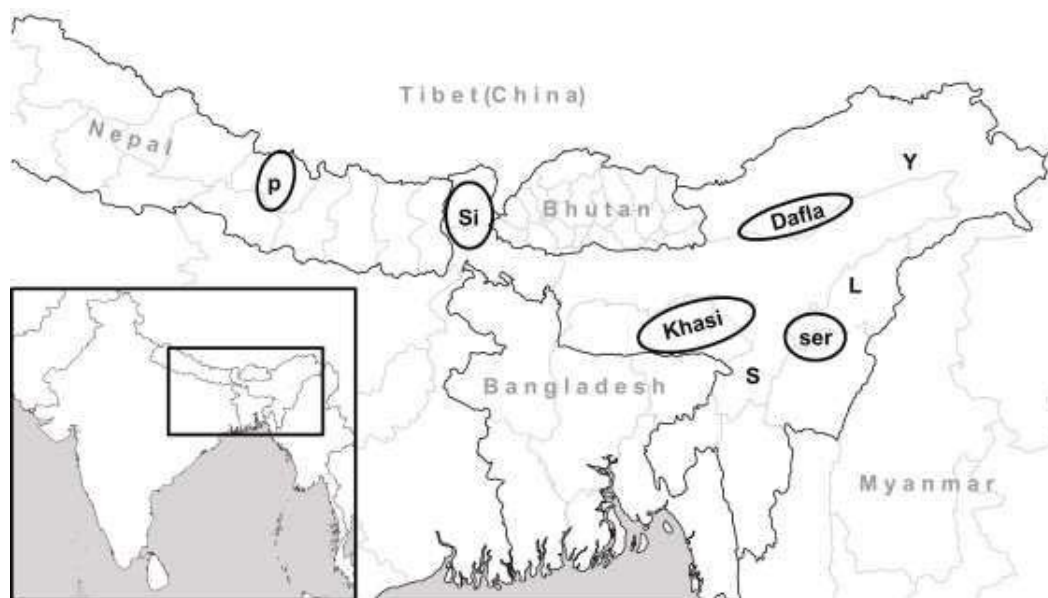


Figure 7.123. Distribution of *Endothyrella* species in Northeast India. Abbreviations: Dafla: Dafla Hills (locality of *E. macromphalus*); Khasi: Khasi Hills (locality of *E. affinis*, *E. fultoni*, *E. species7 u. sp.*, *E. macromphalus*, *E. nomenovum1* nom. nov. and *E. sowerbyi*); L: Lhota Naga (locality of *E. species7 n. sp.*); P: Nepalese localities of *E. nomenovum1* nom. nov.; SER: *Endothyrella serica* (Godwin-Austen 1875); S: Silchar (possibly erroneous locality of *E. blanda*); SI: Sikkim (locality of *E. blanda*, *E. pinacis*, *E. nomenovum1*); Y: Yamne valley (type locality of *E. macromphalus gregorsoni*).

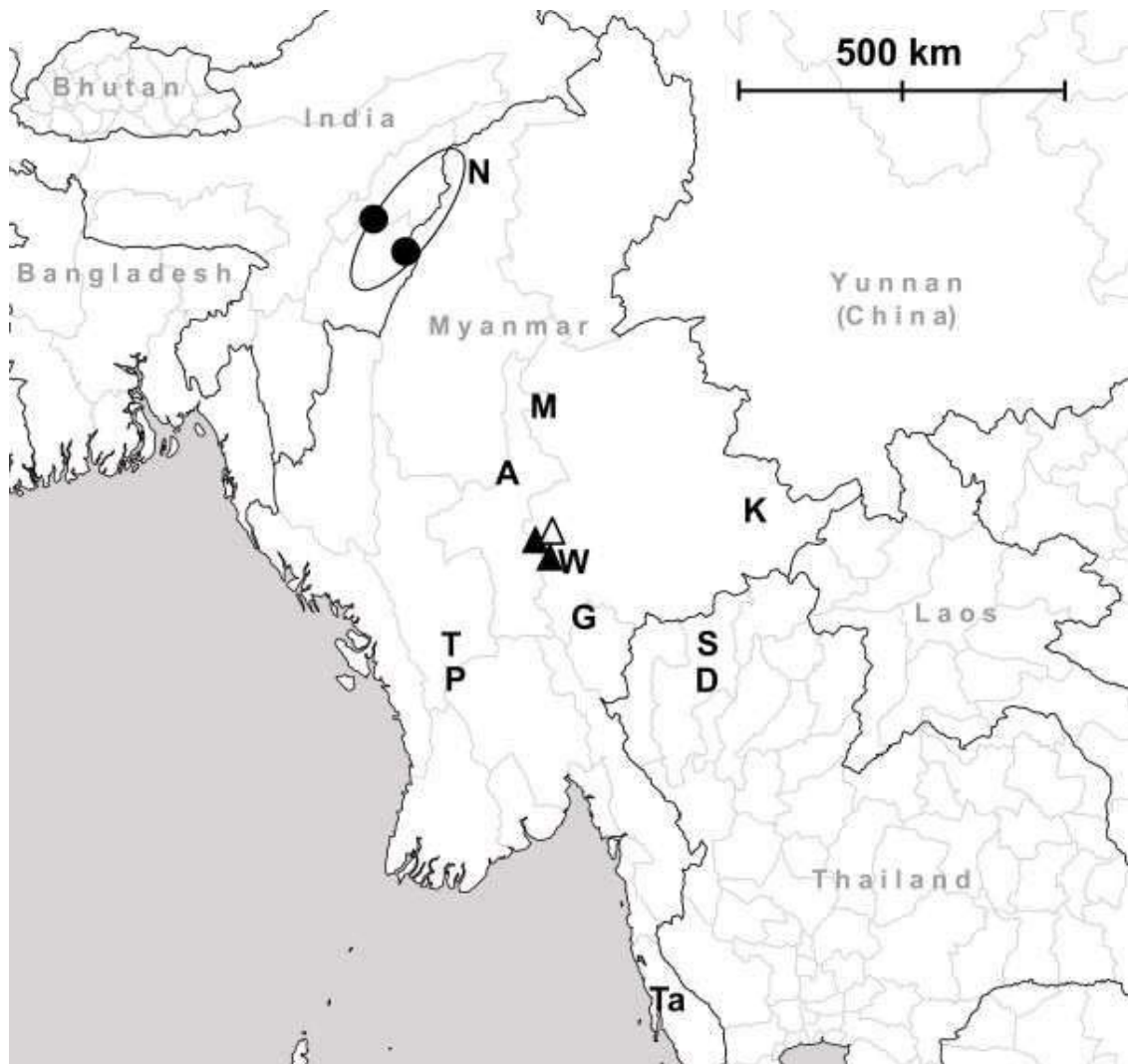


Figure 7.124. Distribution of *Chersaecia* species. Filled circle: *Ch. shiroiensis*; Filled triangle: new localities of *Ch. shanensis*; Empty triangle: new locality of *Ch. perrierae*. Abbreviations: A: Ava (type locality of *Ch. perarcta*); D: type locality of *Ch. degerbolae* (synonym of *Chersaecia refuga*); G: Pekon (type locality of *Chersaecia goniobathmos*); K: Keng Tung (type locality of *Ch. kengtungensis*); M: Mogoke (type locality of *Ch. species1*); N: The oval area shows the Naga Hills (type locality of *Plectopylis nagaensis* and *P. muspratti*); P: Prome (Pyay; type locality of *Ch. feddeni*); S: type locality of *Ch. perarcta simplex*; T: Thyet Myo (type locality of *Ch. perrierae* and *Plectopylis pseudophis*); Ta: Tavoy (Davey; type locality of *Ch. refuga*); W: type locality of *Chersaecia woodthorpei*.

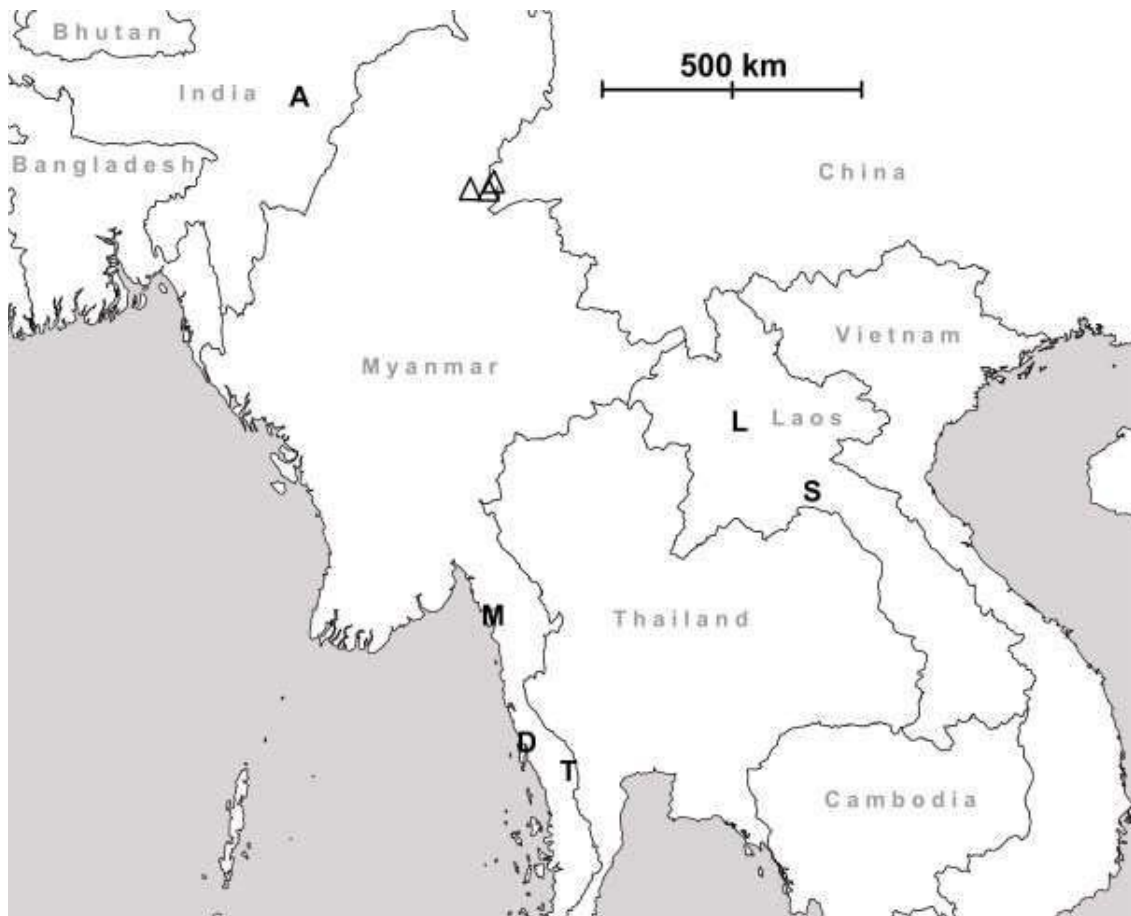
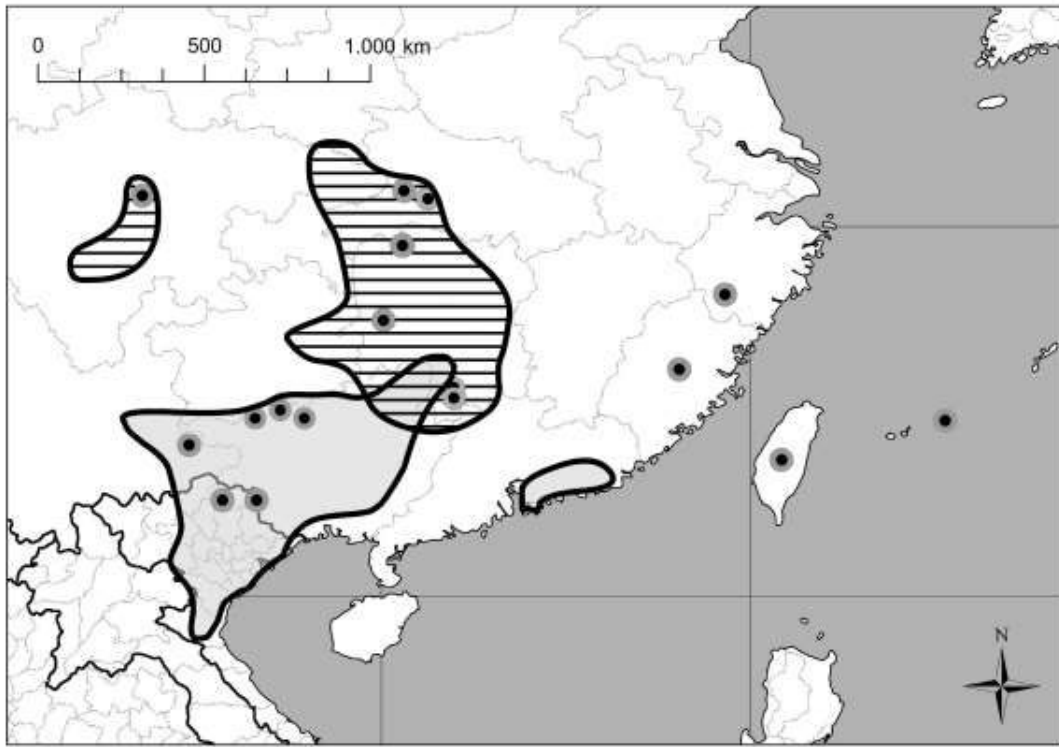


Figure 7.125. Distribution of Genus2, Genus1, *Endoplon* and Genus3 species. Empty triangles: Genus2 *andersoni* (W. Blanford 1869). Abbreviations: A: Diyung valley (type locality of Genus1 *austeni*); D: Tavoy (Davey; locality of Genus1 *dextrorsa*); L: Genus3 *laomontana*; M: Moulmein (type localities of *Endoplon brachyplecta* and *E. smithiana*, and locality of Genus1 *dextrorsa*); S: Genus2 species3; T: Tenasserim (locality of Genus1 *dextrorsa*).



Figure 7.126. Distribution of *Plectopylis* species. Filled circle: *Plectopylis* species2 u. sp.; Empty triangle: exact locality of *Plectopylis bensoni*. Abbreviations: D: Damathat (Dhammasa) (locality of *Plectopylis anguina*); H: Henzada (Hinzhada) (locality of *Plectopylis karenorum*); M: Moulmein (locality of *Plectopylis anguina*, *P. bensoni*, *P. cyclaspis* and maybe *P. karenorum*); Me: Mergui (Myeik) (locality of *Plectopylis anguina* and *P. bensoni*); P: Pegu (Bago) (locality of *Plectopylis karenorum* and *P. lintera*); R: Rangoon (Yangon) (locality of *Plectopylis anguina*); T: Tavoy (Davey) (locality of *Plectopylis anguina* and *P. bensoni*).



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Figure 7.127. Distribution of *Gudeodiscus* (grey shaded area), *Sinicola* Gude 1899 (ruled area) and *Sicradiscus* (circle) species (only exact locality data were used).

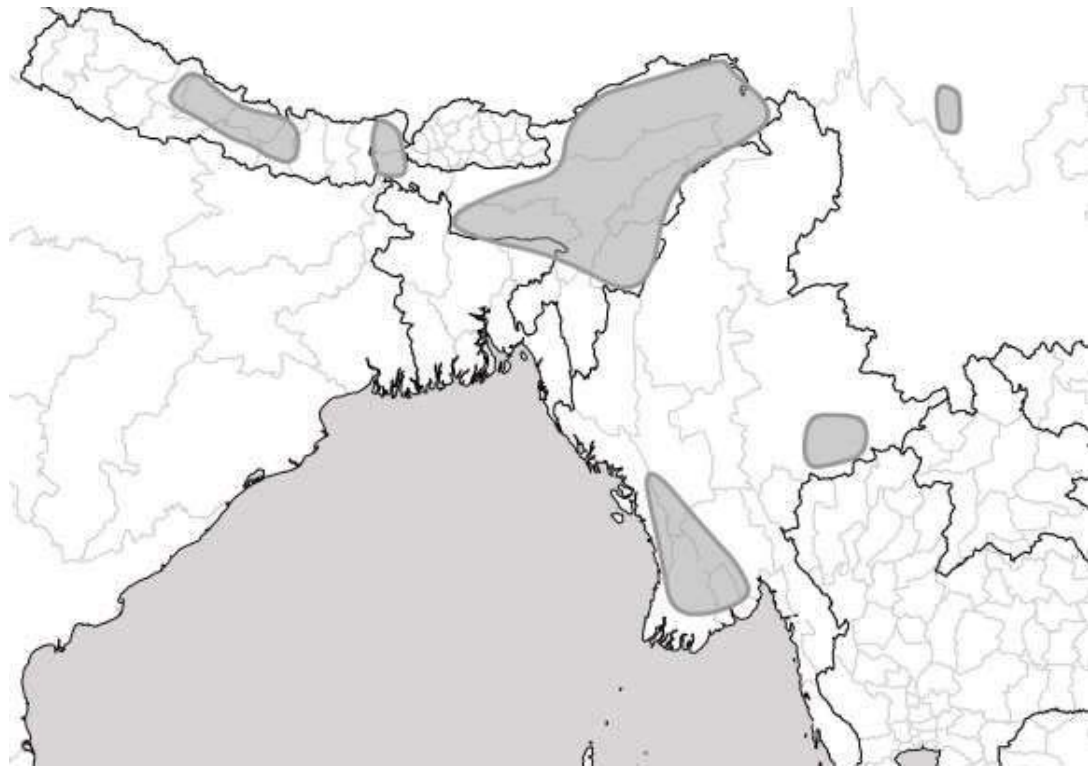


Figure 7.128. Distribution of the genus *Endothyrella*.

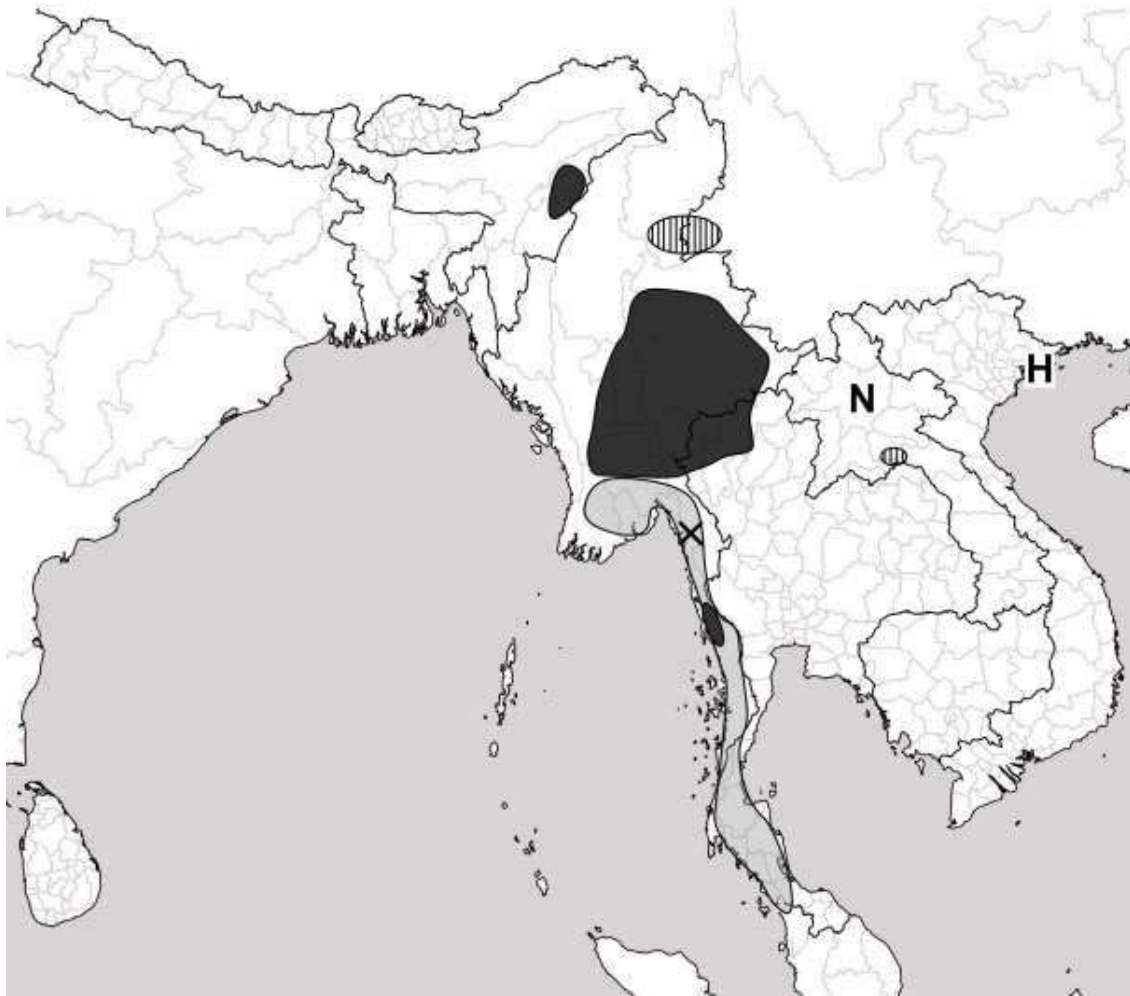


Figure 7.129. Distribution of the genera Genus2 (stripped area), *Chersaecia* (dark shaded area), *Halongella* (letter "H"); Genus3 (letter "N") and *Plectopylis* (light shaded area). X shows the distribution of *Endoplona* taxa.

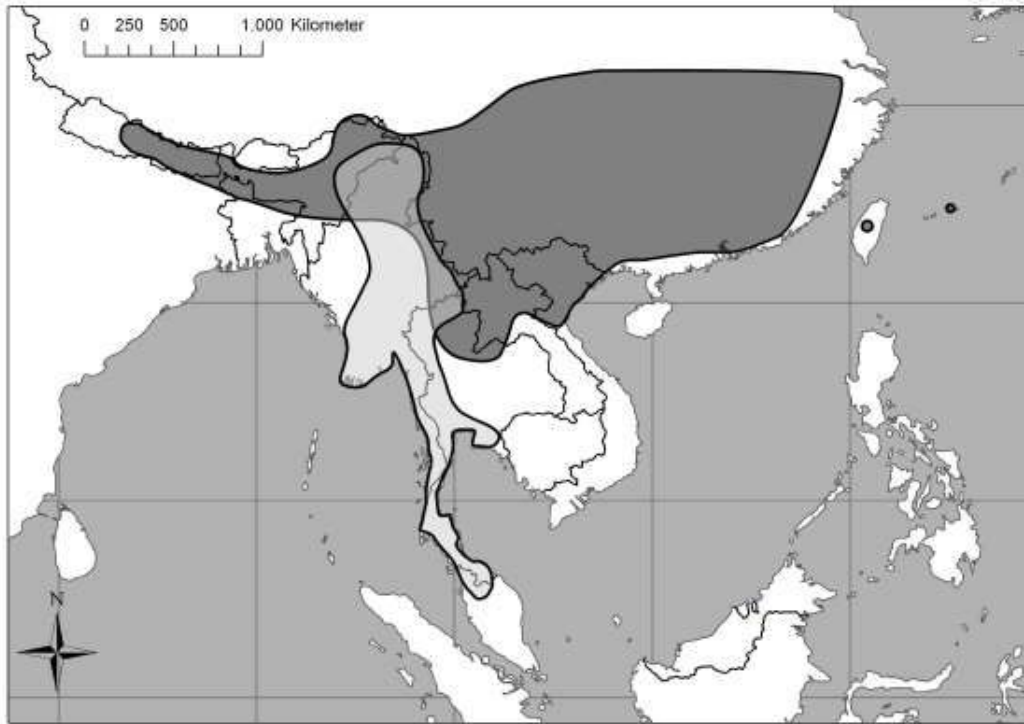


Figure 7.130. Distribution of Tribe1 (light shaded area) and Tribe2 (dark shaded area).

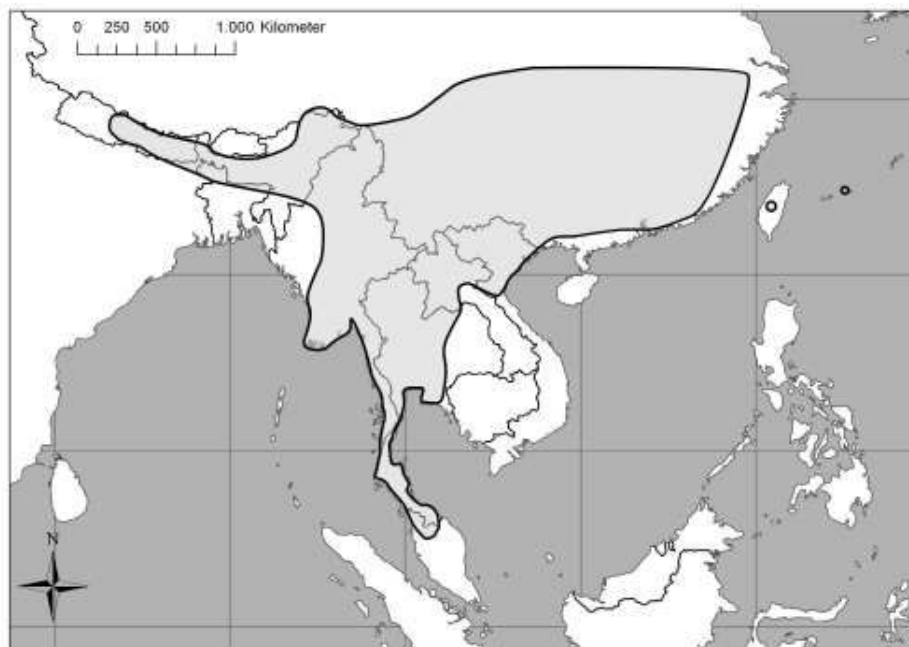


Figure 7.131. Distribution of the family Plectopylidae (after Gude 1899b, Pilsbry 1904, Kuroda 1941 and my data).

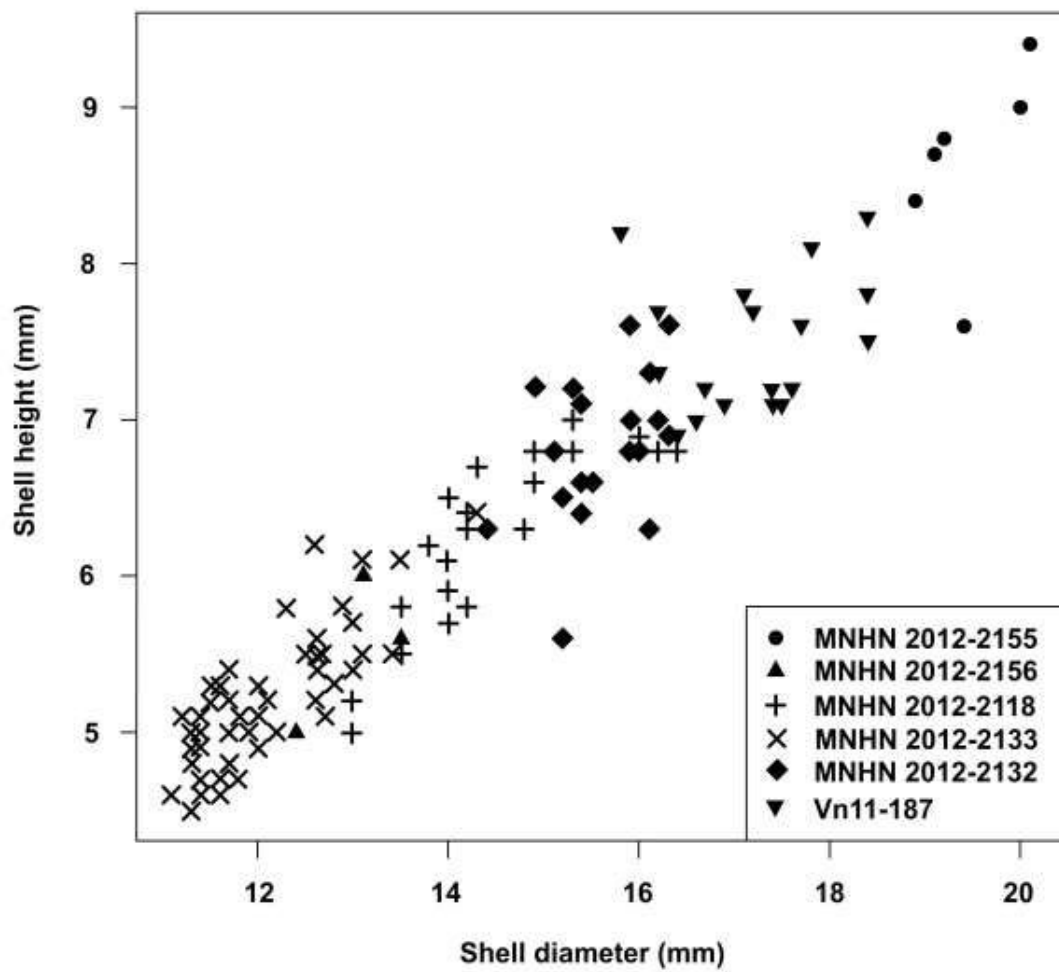


Figure 7.132. Plot of shell height against shell width (diameter) for 122 adults of *Plectopylis* cf. *anteridesgouldingi* (MNHN 2012-2133, MNHN 2012-2156, partly MNHN 2012-2218), *Plectopylis* cf. *fallax* (Vn11-187, MNHN 2012-2132, partly MNHN 2012-2218) and *Plectopylis* cf. *fallax* var. *major* (MNHN 2012-2155) from Northern Vietnam. Samples MNHN 2012-2155 and MNHN 2012-2156 originally belonged to the same sample.



Figure 7.133. 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* (Morelet 1886) (B), Halong Bay area, Vietnam. Photos: F. Naggs.

Table 7.1. Association between the presence of calcareous granules in the penis and embryos in the uterus in the genera of "Eastern Plectopylidae".

Name	Country, province	elevation	date	embryos	shape of granules	No. of specimens
<i>G. emigrans otanii</i>	China, Guangxi	180	November 13	present	no granules	2
<i>G. eroessi eroessi</i>	China, Guangxi	153	November 9	present	no granules	2
<i>G. fischeri</i>	Vietnam, Tuyên Quang	70	March 19	absent	hook-like	1
<i>G. fischeri</i>	Vietnam, Bắc Kạn	335	November 19	present	no granules	1
<i>G. giardi giardi</i>	Vietnam, Cao Bằng	430	November 16	absent	hook-like	1
<i>G. giardi giardi</i>	China, Guangxi	308	January 10	absent	flat, oval	1
<i>G. messengeri raheemi</i>	Vietnam, Hòa Bình	1120	October 15	present	no granules	1
<i>G. multispira</i>	China, Guangxi	160	October 14	present	no granules	3
<i>G. multispira</i>	China, Guangxi	252	November 12	present	no granules	1
<i>G. okuboi</i> , specimen1	China, Guangxi	131	November 9	present	no granules	1
<i>G. okuboi</i> , specimen2	China, Guangxi	131	November 9	absent	no granules	1
<i>G. phlyarius</i>	Vietnam, Lạng Sơn	370	April 1	present	no granules	1
<i>G. phlyarius</i>	China, Guangxi	190	October 11	absent	hook-like	1
<i>G. phlyarius</i>	China, Guangxi	360	October 23	present	no granules	1
<i>G. phlyarius</i> ("fallax")	Vietnam, Lào Cai	270	October 4	absent	flat, oval	2

<i>G. pulvinaris pulvinaris</i>	Hong Kong	300-500	June	absent	hook-like	1
<i>G. pulvinaris robustus</i>	China, Guangxi	140	October 17	present	no granules	1
<i>G. villedaryi</i>	Vietnam, Thái Nguyên	365	May 20	present	no granules	1
<i>G. villedaryi</i>	Vietnam, Thái Nguyên	365	November 12	absent	hook-like	1
<i>Sch. fruhstorferi</i>	Vietnam, Quảng Ninh	20	August 14	present	very thin, flat, no particular shape	1
<i>Sch. schlumbergeri</i>	Vietnam, Hải Phòng	20	April 4	present	flat, thin, with no particular shape	1
<i>Sch. schlumbergeri</i>	Vietnam, Hải Phòng	?	November 22	absent	flat, thin, with no particular shape, or T-shaped	1
<i>Sic. invius</i>	China, Sichuan	1087	September 17	absent	no granules	2
<i>Sic. mansuyi</i>	Vietnam, Cao Bằng	570	May 28	present	no granules	2
<i>Sic. schistoptychia</i>	China, Hunan	450	November 11	present	tiny flat rounded granules	1
<i>Sic. transitus</i>	China, Guangxi	650	September 12	absent	minute, flat, rounded	1
<i>Sin. asamiana</i>	China, Sichuan	860	September 16	present	no granules	1
<i>Sin. emoriens</i>	China, Guangxi	125	November 8	present	no granules	2
<i>Sin. fimbriosa</i>	China, Hunan	590	October 20	absent	no granules	1
<i>Sin. murata</i>	China, Sichuan	860	September 16	present	no granules	1

<i>Sin. murata</i>	China, Sichuan	1090	September 17	present	no granules	1
<i>Sin. reserata azona</i>	China, Guizhou	863	May 10	present	no granules	1
<i>Sin. stenochila</i>	China, Hubei	220	November 3	absent	globular or elongated	2

Table 7.2. 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 7.3. Association of the presence of embryo and the absence of granules within all four genera (*Gudeodiscus*, *Halongella*, *Sicradiscus*, *Sinicola*).

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

Table 7.4. Key characters of the radula of Plectopylidae species. Abbreviations: L: lateral; M: marginal.

	L	M	size of central	shape of the first lateral	morphology of the marginals
<i>Chersaacia perrieriae</i>	8	12	smaller than the ectocone of the first lateral	romboid, or slender with parallel, straight margins and pointed end	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Chersaacia shanensis</i>	8	14	smaller than the ectocone of the first lateral	slender romboid, rather pointed	mostly bicuspid, some of them "show a tendency" to become tricuspid
Genus1 <i>dextrorsa</i>	9	17	smaller than the ectocone of the first lateral	romboid, rather blunt	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Endothyrella blanda</i>	6	14	larger than the ectocone of the first lateral	triangular	tricuspid with pointed cusps and deep incision between them, some of them quadricuspid

<i>Endothyrella fultoni</i>	14	at least 18	larger than the ectocone of the first lateral	elongated romboid, rather blunt	endocones deformed rhomboid (or oval), showing the sign of becoming bicuspid; ectocones blunt or pointed triangular.
<i>Endothyrella fultoni</i>	8	14	as large or larger than the ectocone of the first lateral	oval or narrow-based triangular	tricuspid with pointed cusps and deep incision between them
<i>Gudeodiscus (Veludiscus) emigrans otanii</i>	9	11	slightly smaller than the ectocone of the first lateral	romboid, rather blunt	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Gudeodiscus (Veludiscus) okuboii</i>	7	13	slightly smaller than the ectocone of the first lateral	romboid, rather blunt	tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Gudeodiscus (Veludiscus) pulvinaris pulvinaris</i>	7	14	smaller than the ectocone of the first lateral	romboid, rather blunt	tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Gudeodiscus (Gudeodiscus) eroessi</i>	10	10	smaller than the ectocone of the first lateral	romboid, rather blunt	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Gudeodiscus (Gudeodiscus) fischeri</i>	9	13	as large as or larger than the ectocone of the first lateral	romboid, pointed	tricuspid, inner two rather blunt, incision between them deep
<i>Gudeodiscus (Gudeodiscus) giardi</i>	12	15	as large as the ectocone of the first lateral	romboid, pointed	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Gudeodiscus (Gudeodiscus) messengeri raheemi</i>	8	16	as large as or larger than the ectocone of the first lateral	romboid, pointed	tricuspid with rather sharp inner cusp and deep incision between the cusps
<i>Gudeodiscus (Gudeodiscus) multispira</i>	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
<i>Gudeodiscus (Gudeodiscus) phlyariius</i>	9	12	as large as the ectocone of the first lateral	romboid, pointed	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Gudeodiscus (Gudeodiscus) villedaryi</i>	9	10	as large as or slightly smaller than the ectocone of the first lateral	romboid, pointed	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps

<i>Halongella fruhstorferi</i>	8	12	much smaller than the ectocone of the first lateral	slender romboid	mostly bicuspid, some of them tricuspid with blunt inner cusps
<i>Halongella schlumbergeri</i>	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
Genus3 <i>laomontana</i>	8	12	not visible, probably missing	romboid, rather blunt	mostly bicuspid, some of them "show a tendency" to become tricuspid
<i>Plectopylis bensoni</i>	9	17	smaller than the ectocone of the first lateral	romboid, pointed	mostly bicuspid, some of them "show a tendency" to become tricuspid
<i>Plectopylis species2</i>	9	13	smaller than the ectocone of the first lateral	romboid, pointed	bicuspid or tricuspid with blunt inner cusp and shallow incision between the inner two cusps
<i>Sicradiscus invius</i>	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
<i>Sicradiscus mansuyi</i>	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
<i>Sicradiscus schistoptychia</i>	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
<i>Sicradiscus transitus</i>	6	10	as large as the ectocone of the first lateral	triangular	tricuspid with pointed cusps and deep incision between them
<i>Sinicola asamiana</i>	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
<i>Sinicola emoriens</i>	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
<i>Sinicola fimbriosa</i>	10	15	larger than the ectocone of the first lateral	slender with concave inner line	tricuspid with pointed cusps and deep incision between them

<i>Sinicola jugatoria</i>	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
<i>Sinicola murata</i>	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
<i>Sinicola reserata azona</i>	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
<i>Sinicola stenochila</i>	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

Table 7.5. 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 <i>fischeri</i>
20090519B	weak	normal	connected	2	very thin, translucent, yellowish	OAE	small
2011/96=2011/91=2009.05.17 A=Vn10-28A	weak	normal	not in contact	5	thin, translucent, corneous	elevated	typical <i>tenuis</i>

Table 7.6. Diversity of shell characters within *Gudeodiscus (Gudeodiscus) messengeri raheemi* u. ssp.

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	exceeds lamella	2
20080509C	yellowish-corneous	slightly elevated	normal	exceeds lamella	1
2007.11.16C=2011/106	dark yellow	very slightly elevated	dissolved	exceeds lamella	2

Vn12-104=Vn10-103, 2012/60	light or dark brown	slightly elevated	normal or dissolved	reaches or exceeds lamella	4
20071118A	dark brown	slightly elevated	dissolved	exceeds 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

Table 7.7. Diversity of shell characters within 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

Table 7.8. Diversity of shell characters within *Gudeodiscus* (*Gudeodiscus*) *suprafilaris*. Abbreviations: OCMA: only corroded material available.

sample	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

Table 7.9. Diversity of shell characters 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

Table 7.10. Localities of Genus1, *Chersaecia*, *Endoplou*, *Endothyrella* and *Plectopylis* species mentioned in the literature and on museum labels. Abbreviation: ELU: Exact locality unknown.

locality	region	taxon	Remarks
Abor Hills	India: Arunachal Pradesh	<i>williamsoni</i>	
Akouktoung	Myanmar: "below Prome"	<i>feddeni</i>	ELU
Arakan Hills (=Rakhine)	Myanmar: Rakhine district	<i>plectostoma</i>	
Attaran River	Myanmar, Mawlamyine	<i>smithiana</i>	
Ava (Inwa)	Myanmar: Mandalay district: 21° 51'N 95° 59'E	<i>perarcta</i>	
Bassein (=Patheingyi)	Myanmar, Ayeyarwady district: 16°47'N, 94°44'E	<i>plectostoma</i>	
Bhamo	city in Myanmar, Kachin State: 24° 16'N 97° 14'E	<i>andersoni</i>	
Brahmakund	India: Assam, 27°51.4'N, 96°22'E	<i>brahma</i>	
Burrail (=Barail) Gorge	India: mountain range centered 70 km ne Silchar (Assam)	<i>plectostoma</i> , <i>macromphalus</i>	

Cachar (Katchar)	India: District in Assam: 24°46'N, 92°50'E	<i>affinis, serica, plectostoma, blanda</i>	
Cherra Poonjee (Cherrapunji)	India: Meghalaya: Khasi Hills: 25°18'N, 91°42'E	<i>affinis, fultoni, plectostoma</i> and <i>p. exerta</i>	
Damathat Hill (probably Dhammasa)	Myanmar: Bago District: 16° 30.6'N 97° 49'E	<i>anguina</i>	
Damsang Peak	India: Sikkim: 27° 9'N 88° 36.5'E	<i>blanda, pinacis</i>	
Darjiling (Darjeeling)	India: town in West Bengal: 27°2'N, 88°15.5'E	<i>blanda, macromphalus, nomenovum1, pinacis, plectostoma</i>	
Dihang (Siang) River	India: Arunachal Pradesh: river flows to the Brahmaputra at 27°50'N, 95°27'E	<i>bedfordi, oakesi</i>	
Diyung Valley	River in India: Sikkim, tributary of the Brahmaputra, flows to in near 26° 34'N 93° 50'E	<i>austeni</i>	
Doi Sutep	Mountain in North Thailand: 18° 49'N 98° 54'E	<i>degerbolae</i>	
Dunsiri River	India: river in Nagaland?	<i>plectostoma</i>	ELU
Durrang	India: probably Dafla Hills	<i>plectostoma</i>	ELU
Fort Stedman (Maing Thauk)	Myanmar: Southeastern Shan Region: 20° 34.5'N 96° 56'E	<i>woodthorpei</i>	
Garo Hills	India: Western Meghalaya: 25° 28'N, 90°20'E	<i>plectostoma</i>	
Hengdan	India: mountain in North Cachar Hills	<i>serica</i>	ELU
Henzada (Hinthada)	district and town (17° 39'N 95° 28'E) on the borders of Bago and Ayeyarwady Regions, Myanmar	<i>karenorum</i>	
Hlindet	Burma	<i>feddeni (ponsonbyi)</i>	ELU
Hoetone (Hutung)	Myanmar: Kachin State: 24° 15'N 97° 32'E	<i>andersoni</i>	
Ihang River	India: Manipur	<i>species7 u. sp., serica</i>	ELU
Japvo Peak	India: highest mountain in Naga Hills: 25°36'N, 94°4'E	<i>shiroiensis, serica</i>	
Kaintha	village in Hinthada district, on the borders of Bago and Ayeyarwady Regions, Myanmar	<i>karenorum</i>	
Kakhyen Hills	ills along the Burmese/Chinese border SW of Yingjiang: 24°27' N 97°34' E	<i>andersoni</i>	
Kengtung (Keng Tung)	Myanmar: Eastern Shan Region: 21° 17'N 99° 36'E	<i>leiophis (kengtungensis)</i>	
Khasi Hills	India: Meghalaya	<i>affinis, fultoni, macromphalus, nomenovum1, pinacis (?) , plectostoma, pl. exerta, sowerbyi</i>	
Khunho (Khono?) Mountain	India: Naga Hills	<i>serica</i>	ELU
Kohima	India: town in Southeastern Nagaland: 25°40'N, 94°6.5'E	<i>serica</i>	
Kopamedza ridge	India: Dafla Hills: Barail Range	<i>serica</i>	ELU
Kwadouk	near Thyet Mio	<i>leiophis</i>	ELU

Kyengdwen River	Myanmar	<i>perrierae</i>	ELU
Lahupa	India: Naga Hills	subspecies1?	ELU
Laisen Peak, Manipur	India: Manupur	species7 u. sp.	ELU
Lhota Naga	India: Nagaland: Naga Hills	species7 u. sp.	ELU
Luang Prabang	City in Laos: 19° 53.5'N102° 9'E	<i>laomontana</i>	
Luyor Peak	India: Abor county: Arunachal Pradesh: 28°45'N, 95°45'E	<i>babbagei</i>	
Mairung (Mairang)	India: village in Meghalaya, Khasi Hills: 25°34.2'N, 91°37.8'E	<i>macromphalus</i>	
Manko	"near Newville", Myanmar: Tanintharyi Region	<i>anguina</i>	ELU
Mergui (=Myeik)	city in Myanmar: Tanintharyi Region: 12° 26'N 98° 36'E	<i>anguina, feddeni</i>	
Miri Hills	India: on the border between Assam and Arunachal Pradesh	<i>miriensis</i>	
Mogok (Mogoke)	Myanmar: Mandalay Region: 22° 55'N 96° 30'E	species1	
Moulmein (=Mawlamyine)	City in Myanmar, Mon State: 16° 29'N 97° 37'E	<i>dextrorsa</i>	
Mulé-it Range	east of Moulmein, Tenasserim	<i>dextrorsa</i>	ELU
Manipur (Manipur)	India: Manipur	species7 u. sp., <i>plectostoma, serica</i>	
Myaleit doung	"near Ava"	<i>perarcta</i>	ELU
		<i>serica, blanda, macromphalus</i> (?), species7 u. sp., nomen novum1 (?), <i>plectostoma</i>	
Naga Hills	India: on the border of Nagaland (India) and Myanmar		
Naraindher	India: Assam: Cachar district	<i>affinis</i>	ELU
Newville	"province of Tavoy"	<i>anguina</i>	ELU
Nioung jo	Burma?	<i>feddeni</i>	ELU
Nungatho Khyoung	Myanmar, Henzada (Hinthada) District	<i>karenorum</i>	ELU
Pah Hia	Laos, approx. 100 km south of Xiangkhouang	species3	ELU
Pankabari (Pankhabari)	India: northern part of West Bengal: 26°50'N 88°16'E	<i>pinacis</i>	
Pathung-Thoung	"Attaram Region"	<i>linterae</i>	ELU
Pegu (=Bago)	Myanmar: Bago District: 17°20'N, 96°29'E	<i>plectostoma</i>	
Pekon	Myanmar: Southern Shan District: 19° 45'N 97° 5'E	<i>goniobathmos</i>	
Phye-thán	Myanmar, Tenasserim	<i>dextrorsa</i>	ELU
Picholanulla	India: probably Dafla Hills	<i>plectostoma</i>	ELU
Ponsekai	Thailand?	<i>dextrorsa</i>	ELU
Prome (Pyay)	Myanmar: Bago district: 18° 49.5'N 95° 13'E	<i>feddeni</i>	
Prowi	India: Naga Hills	<i>leiophis (nagaensis)</i>	ELU
Pyema Khyoung	Myanmar: Ayeyarwady district	<i>plectostoma</i>	
Rangoon (Yangon)	Myanmar: Yangon district and city: 16° 47'N 96° 9'E	<i>anguina</i>	

Rarhichu (=Rungpo?)	India: Sikkim	<i>blanda,</i> <i>nomen novum1, pinacis</i>	ELU
Renging (=rengging)	India: Abor county: Arunachal Pradesh: 28°9'N, 95°15.5'E	<i>aborensis</i>	ELU
Richila (Rechila) Peak	India, Sikkim: 27°8'N, 88°45'E	<i>blanda</i>	
Rinkpo valley	India: Sikkim	<i>blanda</i>	ELU
Rissetchu	India: Sikkim	<i>blanda</i>	ELU
Riu	India: Abor Hills	<i>oakesi</i>	ELU
Rotung (=Rottung)	India: Abor county: Arunachal Pradesh: 28°8'N, 95°8.5'E	<i>aborensis</i>	ELU
Rungmaval	India: Sikkim	<i>pinacis</i>	ELU
Rungun	India: probably Sikkim	<i>pinacis, nomen novum1</i>	ELU
Sadia (Sadiya)	India: Assam: 27°51.6'N, 95°37.6'E	<i>oglei</i>	
Shillong	India: city in Meghalaya, Khasi Hills	<i>macromphalus</i>	
Shiroifurar peak (probably Shirui Hills)	India: northeastern Manipur: 25° 6.3'N 94° 27.4'E	<i>plectostoma,</i> <i>shiroiensis</i>	
Shweego (Shwegu?)	probably Myanmar: Kachin District: 24°12'N, 96°48'E	<i>plectostoma</i>	
Sibbum (=Sibum)	India: Abor Hills: 28°19'N, 95°9'E	<i>oakesi</i>	ELU
Sigon (Siyom) River	India: river runs into the Siang River at 28°14'N, 95°E	<i>bedfordi</i>	
Sikhami	India: Naga Hills	<i>leiophis</i>	ELU
Singging	India: Abor Hills	<i>oakesi</i>	ELU
Singhpo	India: Assam	<i>austeni</i>	ELU
Sylhet	Bangladesh: Sylhet Division: Sylhet city: 24°54'N, 91°52'E	<i>serica, plectostoma</i>	
Tavoy (Davey)	City in Myanmar: Tanintharyi Region: 14° 5'N 98° 12'E	<i>anguina, bensoni,</i> <i>refuga</i>	
Tenasserim	Myanmar: Tanintharyi Region	<i>dextrorsa</i>	
Teria Ghat	India: Khasi Hills	<i>macromphalus,</i> <i>plectostoma</i>	
Thyet Myo (Thayet)	Myanmar: Magway Region 19° 19.5'N 95° 11'E	<i>feddeni, perrieriae</i>	
Tianoba	Mulé-it Range, Tenasserim	<i>dextrorsa</i>	ELU
Tonghu (Tuonghoo)	Myanmar	<i>feddeni</i>	ELU
Tongoop	Myanmar: Rakhine district	<i>plectostoma</i>	ELU
Torúpútú	India: Dafla Hills	species7 u. sp.	ELU
Tsanda Khyoung	river in Hinthada district, on the borders of Bago and Ayeyarwady Regions, Myanmar	<i>karenorum</i>	ELU
Tsanspu (Tsangpo) River	India (Tibetan name of the Brahmaputra River)	<i>bedfordi</i>	
Yamne River	India: Abor Hills, river flows into the Siang River at 28°10.5'N, 95°13'E	<i>gregorsoni, oakesi</i>	

Chapter 8: Homologies of the parietal plicae and lamellae

Two structures (genes, organs, any morphological features) are homologous when they share a common ancestor. Taxonomists compare putatively homologous morphological structures. In modern biology homology between structures can be hypothesized using multiple techniques, such as gene expression patterns (Niknejad et al. 2012). In case of morphological structures on gastropod shells, however, molecular approaches are not possible. We have to rely on "classic" approaches defined by Remane (1952), who recognized three criteria: (1) the criterion of topological equivalence (similar relative position of structures); (2) the criterion of special quality of structures ("similarity") and (3) the linkage by intermediate forms. The primary and most important of these three is the topology, because as Hennig (1966) argued, the recognition of special quality of structures and intermediate forms requires a primacy of the criterion of topological correspondence (see also Rieppel & Kearney 2002). The inner plicae and lamellae form a very complex structure in every species of Plectopylidae. At first sight it is not obvious which plica or lamella is homologous with which. In the taxonomic history of this family we cannot find hypotheses about their homologies, although most previous authors described the plication very accurately. In the following, I hypothesize homologies among the plicae and lamellae mainly based on their relative similar positions inside the shell (topology). Additionally, I occasionally rely on the similarities in shape and information on ontogeny. Although not stated explicitly, similar approach has been used in taxonomic publications which establish nomenclature of shell characters (e.g. Pilsbry 1927, Nordsieck 1982, 1986, 2007).

Teratological lamellation

In the literature, sometimes the lamellation of abnormal specimens are described. Recognizing the teratological lamellation is very important to recognize traits which help to reveal the homologies of the plicae. In some cases previous authors have not realized that the specimen observed, described and figured by them had teratological lamellae.

Godwin-Austen (1875b) published a drawing of a *Plectopylis feddeni* (Blanford 1865) specimen having three lamellae (Figure 8.1A). Gude (1914) even produced his identification key stating that *feddeni* has "three transverse parietal plates". Contrary to this record, both other specimens of the same sample had only two lamellae (Figure 8.1.B), which is usual in the whole genus.

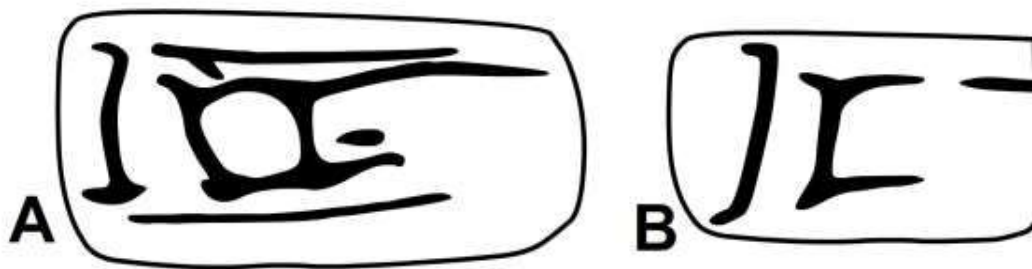


Figure 8.1. A: *Plectopylis feddeni* after Godwin-Austen (1875b); B: *Plectopylis feddeni* specimen from the same sample (after Gude 1914b).

Heude (1885) also published a teratological specimen of *Sinicola biforis* (Heude 1885) with abnormal plication (two straight lamellae, Figure 8.2A). Investigating the original sample revealed that *S. biforis* usually has a single lamella and denticles anteriorly (Figure 8.2B) instead of having two lamellae as depicted by Heude (1885). All other *Sinicola* species has a single lamella occasionally denticles on its anterior side.

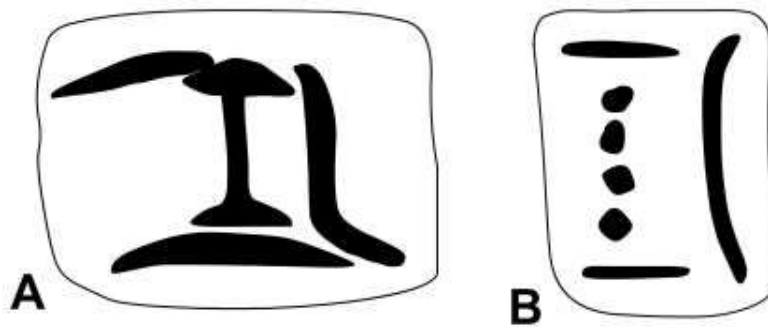


Figure 8.2. A: *Sinicola biforis* after Heude (1885) and B: *Sinicola biforis* syntype specimen examined by me.

The drawing of the parietal lamellae of *Sinicola schistoptychia* (Gude 1897i; Figure 8.3A), namely a single lamella with dichotomously divided lower end, did not corroborate with my observations (Figure 8.3B). All specimens I observed, including the ones probably Gude also had seen, had two vertical lamellae. I assume that Gude did not open the shells and has not seen the parietal lamellae, but published a drawing, which explains the name "schistoptychia", meaning "divided lamella".

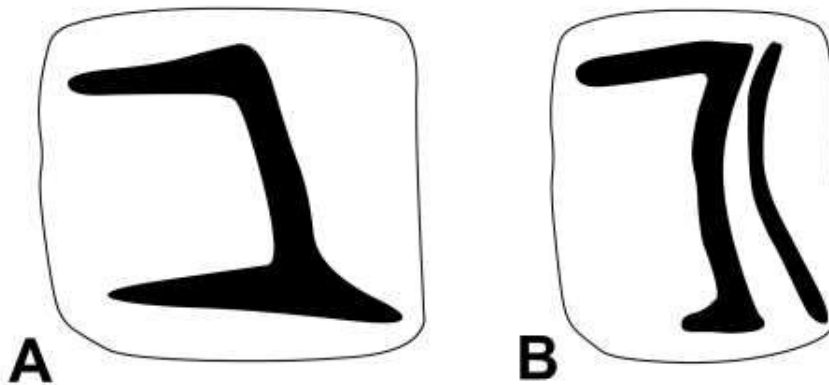


Figure 8.3. A: Parietal lamella of *Sicradiscus schistoptychia* after Gude (1897i), and B: another specimen examined by me (Jiuyishan Guojia Senlin Gongyuan).

In some cases however, previous authors recognized that they are looking at teratological specimens. After the description of *Helix (Plectopylis) serica*, Godwin-Austen (1875) mentioned that "after opening out several specimens (...) I found one shell to have two vertical parietal lamellæ" (Godwin-Austen 1875). Gude (1908b) reported an abnormal specimen of *Gudeodiscus giardi* having four vertical lamellae. Later, he argued that these abnormally multiple lamellae are the "remains of earlier set of barriers" (Gude 1914).

Character states of the parietal plication of Tribe2

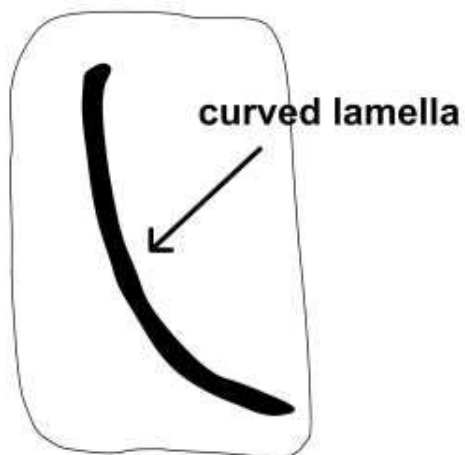


Figure 8.4. (character state A on Figure 8.16). Only one curved lamella is present. This character state can be found in *Genus3 laomontana* and some populations of *Gudeodiscus pulvinaris robustus*.

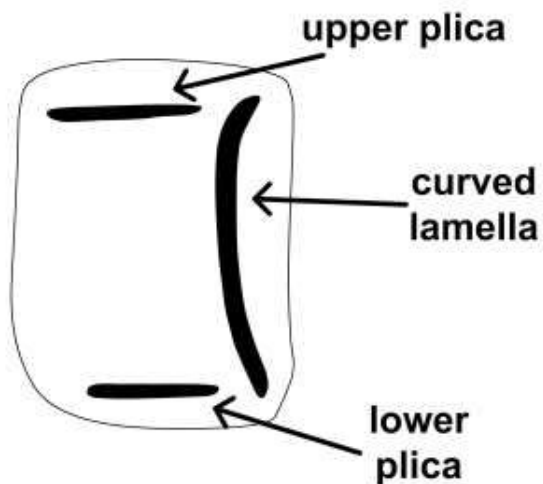


Figure 8.5. (character state B on Figure 8.16). A curved lamella is present, with an upper and a lower plica anteriorly. Both plica are situated close the sutures. Typical for *Sinicola* and *Gudeodiscus* and *Halongella* species.

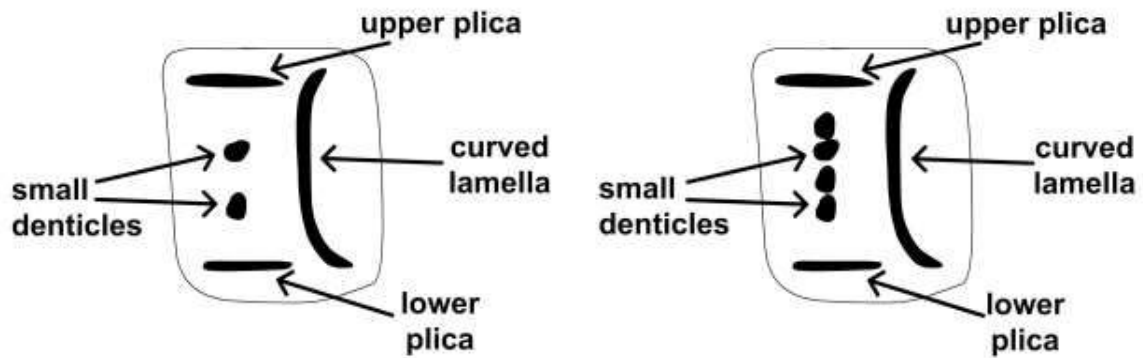


Figure 8.6. (character state C on Figure 8.16). A curved lamella is present, with an upper plica, a lower plica and some small denticles anteriorly. Left image shows two, right image four denticles. Typical for several *Gudeodiscus* and *Sinicola* species.

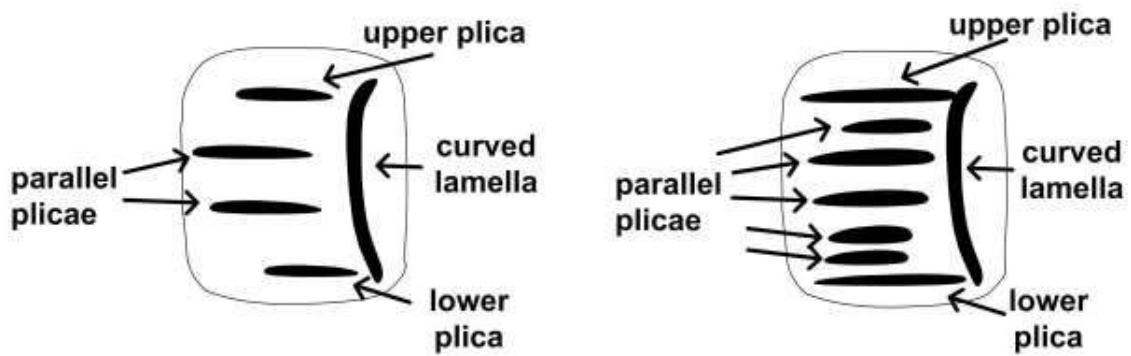


Figure 8.7. (character state D on Figure 8.16). A single curved lamella is present, with some parallel plicae anteriorly. Between the upper and the lower plicae there are 2–4 horizontal, parallel plicae (left image: 2 plicae, right image: 4 plicae). This character state is visible in some *Gudeodiscus* and *Sinicola* species.

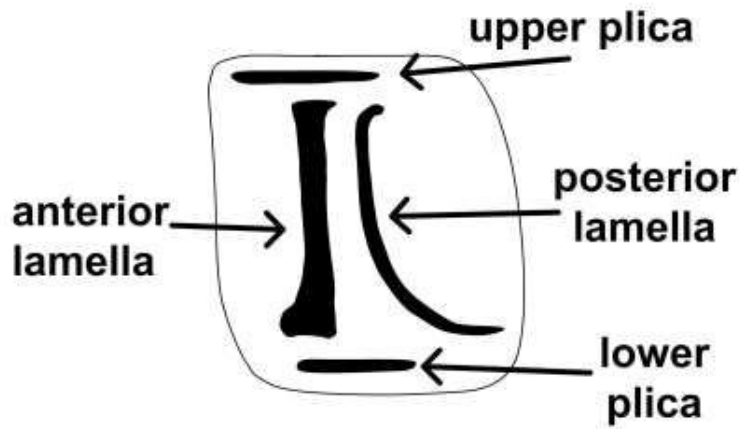


Figure 8.8. (character state E on Figure 8.16). There are two lamellae. The anterior lamella is usually straight and vertical, the posterior lamella is usually curved. The upper plica is situated above, whereas the lower plica below the anterior lamella. Typical in the genera *Gudeodiscus* and *Sicradiscus*.

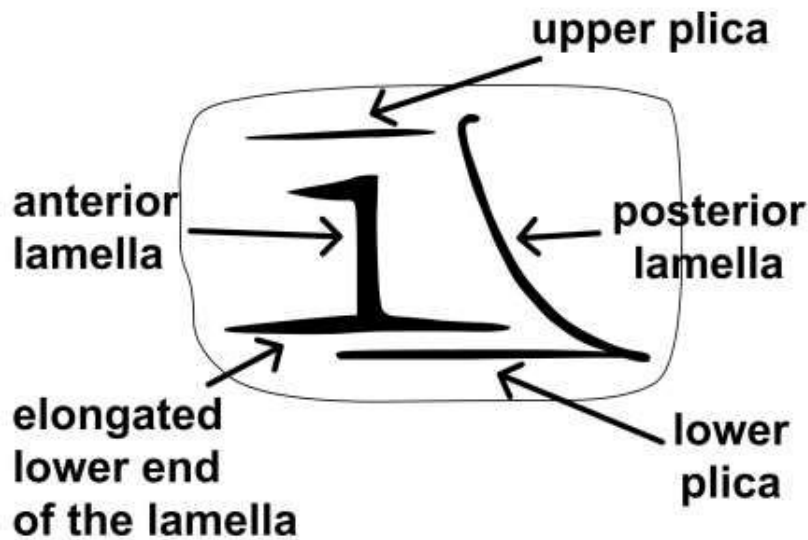


Figure 8.9. (character state F on Figure 8.16). There are two lamellae. The posterior is curved, simple, but the anterior lamella has the lower end elongated anteriorly and posteriorly as well. The upper plica is situated above, whereas the lower plica below the anterior lamella. This character state is present only in *Gudeodiscus villedaryi*.

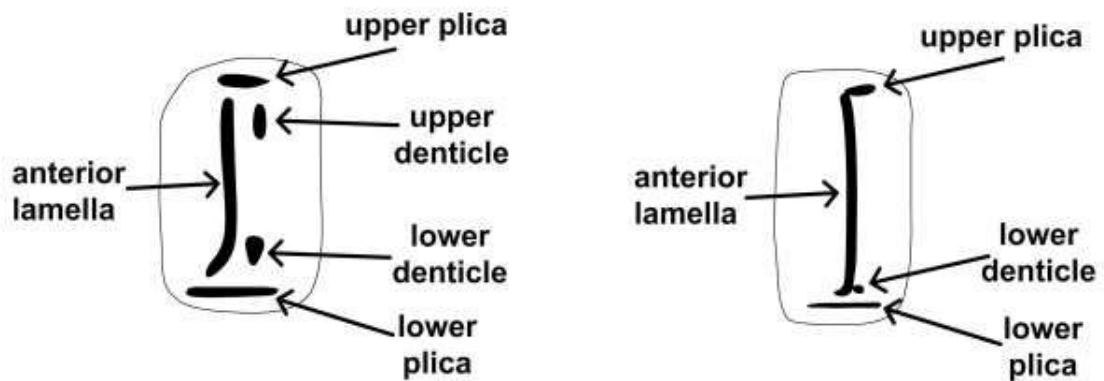


Figure 8.10. (character state G on Figure 8.16). One, more or less straight lamella present (anterior lamella), with upper plica above and lower plica below the lamella. There are small denticles posterior to the lamella, one above (upper denticle) and one below (lower denticle). In the left picture both denticles are present, whereas on the picture on the right the upper denticle is absent. Any of the posteriorly situated denticles can be so close to the lamella that they may be partly fused to it. Typical for *Sicradiscus cutisculptus* and most *Endothyrella* species.

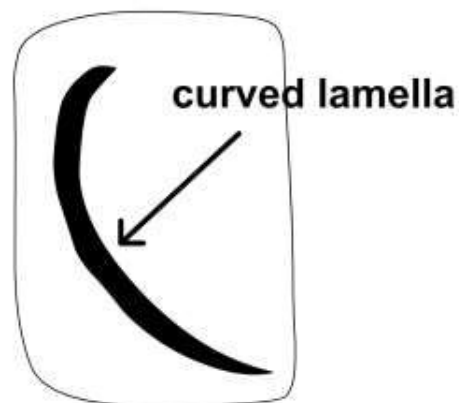


Figure 8.11. (character state H on Figure 8.16). Single, curved lamella, similar to Figure 8.4. This character state is present in *Endothyrella* species6 u. sp. and *E. babbagei*.

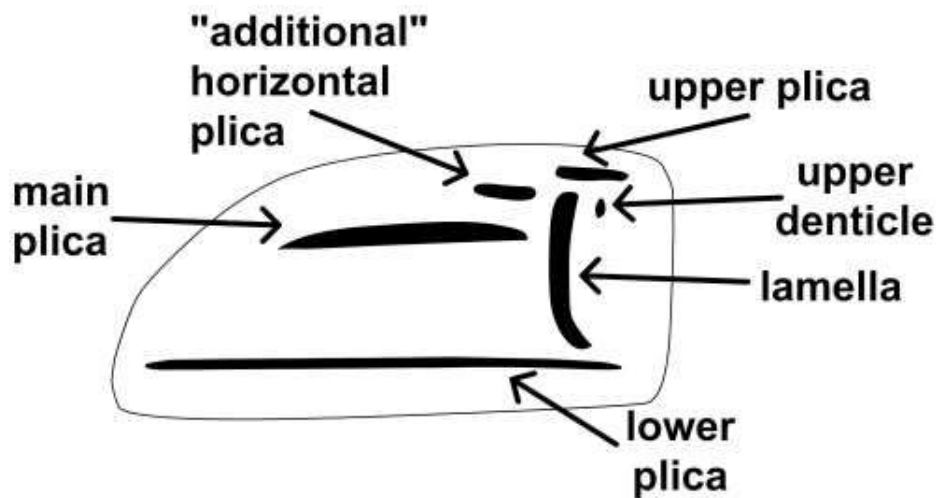


Figure 8.12. (character state I on Figure 8.16). One, more or less straight lamella is present with a small upper denticle posteriorly, and 2-3 horizontal plicae anteriorly. The longest anterior plica is the main plica, the one situated above is named "additional horizontal plica". The long lower plica reaches the peristome. The upper plica is short. This character state is present in *Endothyrella williamsoni* and *E. brahma*. In the latter species the upper denticle is missing.

Character states of the parietal plication of Tribe1

The genera of Tribe1 have three main types of parietal plication. Here I describe these three types and an intermediate character state as the fourth type:

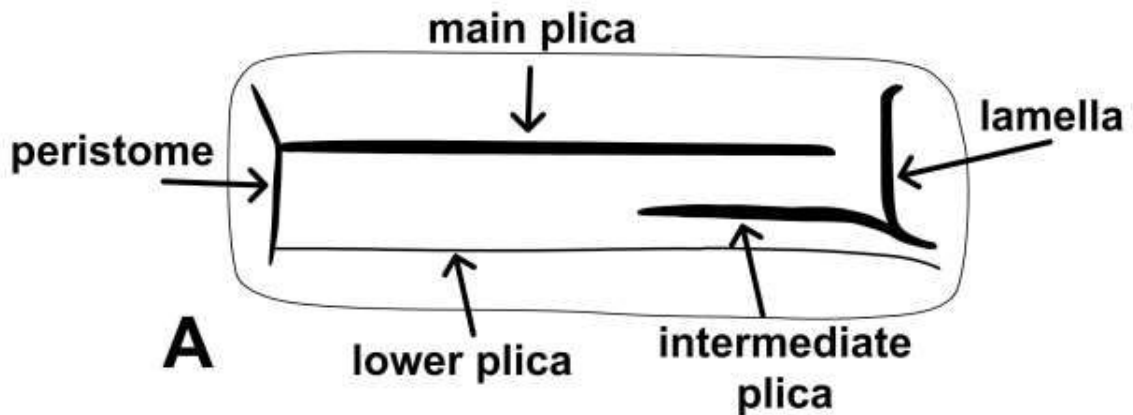


Figure 8.13. (character state J on Figure 8.18). A single lamella, a long main plica, a long lower plica and a short intermediate plica are present. This character state is typical in *Chersaecia*.

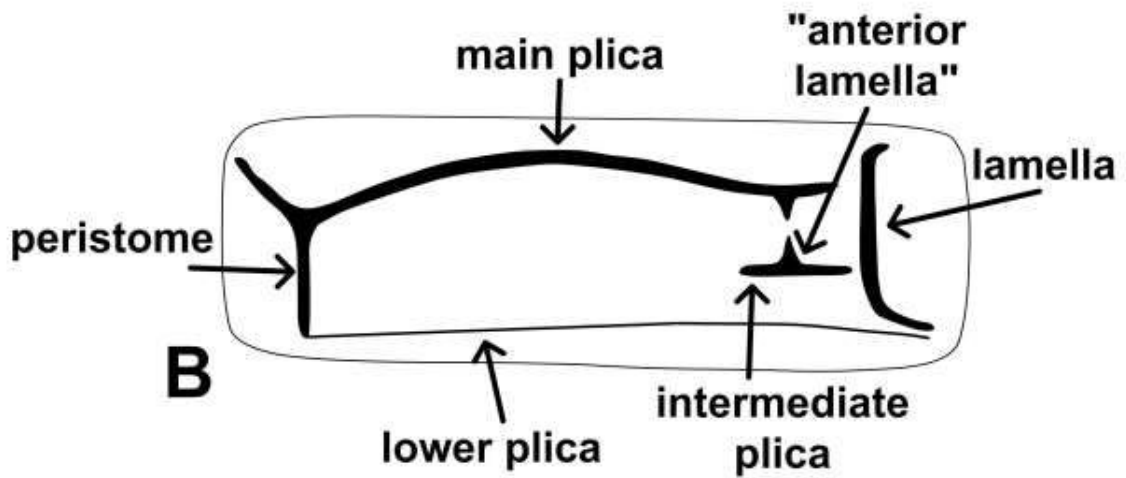


Figure 8.14. (character state K on Figure 8.18). Intermediate character state between those in Figure 8.13. and Figure 8.15. A single lamella, a long main plica, a long lower plica and a short intermediate plica are present. Between the posterior end of the main plica and the intermediate plica there is an interrupted anterior lamella. This character state can be found in some *Chersaecia* specimens.

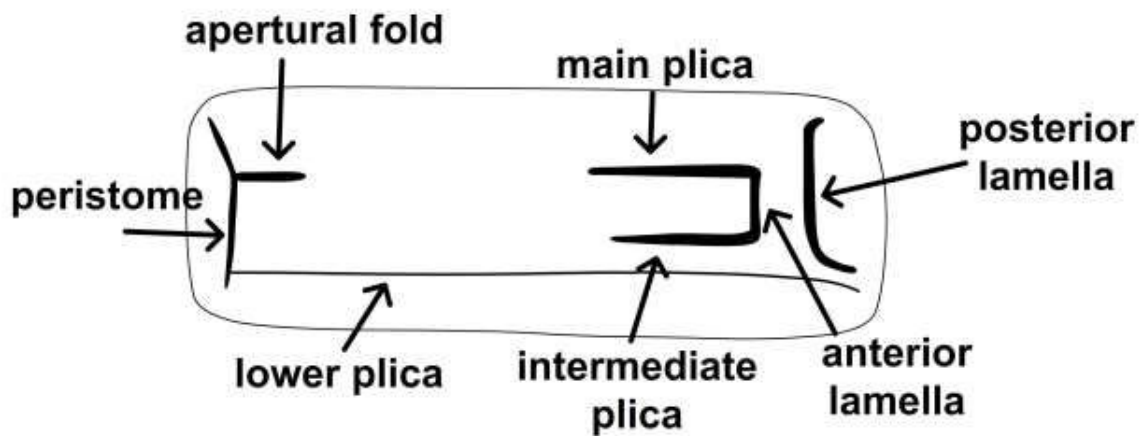


Figure 8.15. (character state L on Figure 8.18). Two lamellae (anterior and posterior), short main plica and intermediated plica, long lower plica are present. An apertural fold is separated from main plica. This character state is present in some *Chersaecia* species, which were classified within *Plectopylis* by Gude (1899e).

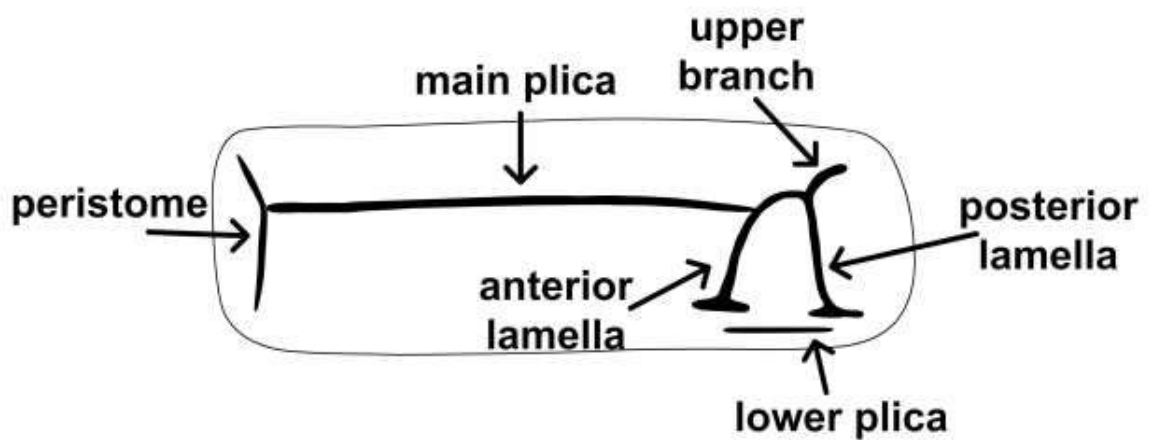


Figure 8.16. (character state M on Figure 8.18). The two lamellae form a complex structure which resembles to the Greek letter lambda (λ). This character state is found in all the species of *Plectopylis*.

Which plica/lamella is homologous with which?

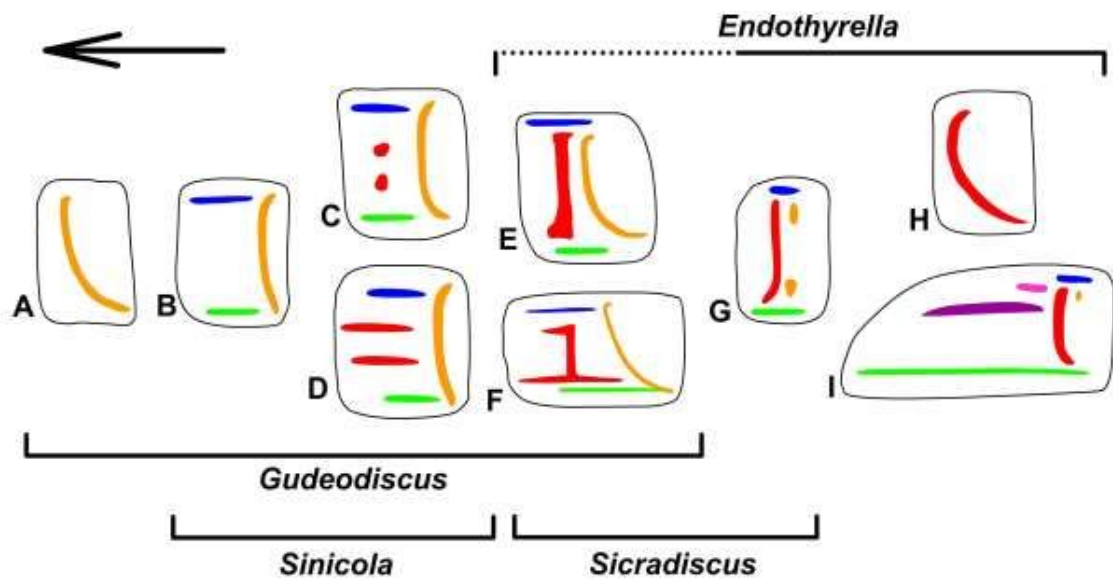


Figure 8.17. Main character states of the parietal plicae and lamellae in genera of Tribe 2. See detailed explanation in the text. Individual images from A to I represent the character states in the four genera. Supposedly homologous structures are indicated with the same colour. The line below *Endothyrella* is partly dashed because *Endothyrella aborensis* is said to have two lamellae (Gude 1915), but I was unable to examine those specimens. The arrow shows the direction of the aperture. Vertical axes is not meaningful.

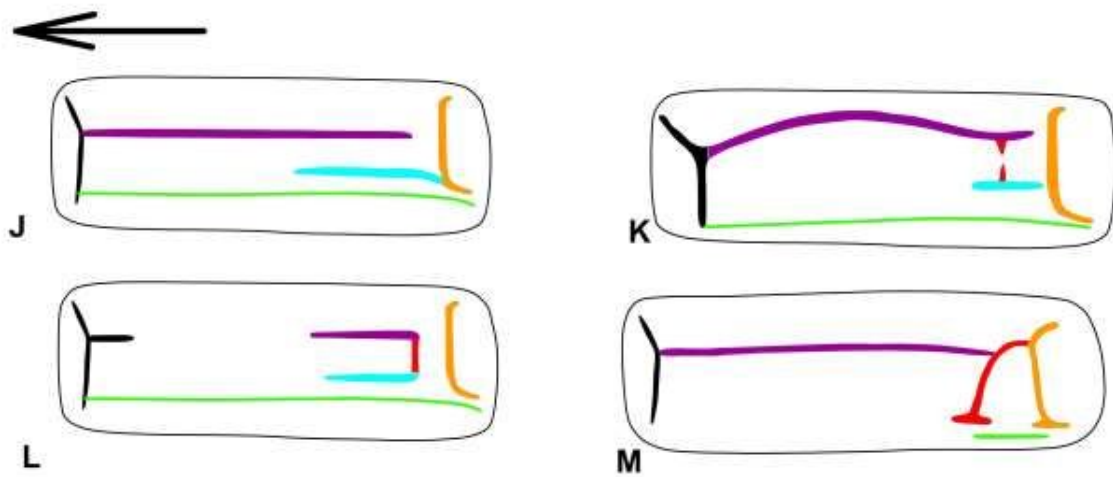


Figure 8.18. Main character states of the parietal plicae and lamellae in genera of Tribe1. See detailed explanation in the text. Individual images from J to M represent the character states in the four genera. Supposedly homologous structures are indicated with the same colours, which also indicate homologies to those in Figure 8.17. In order to make these figures easier to comprehend with those on Figure 8.17, I reversed these drawings in order to show as if they were dextral shells. The arrow shows the direction of the aperture.

In the following, the letters A–M refer to the different character states of the Figure 8.17 and Figure 8.18. Hypotheses of evolutionary relationships among the character states in the two groups were based on the following 15 assumptions:

(1) The denticles of the character state "C" are homologous with the anterior lamella in character state "E".

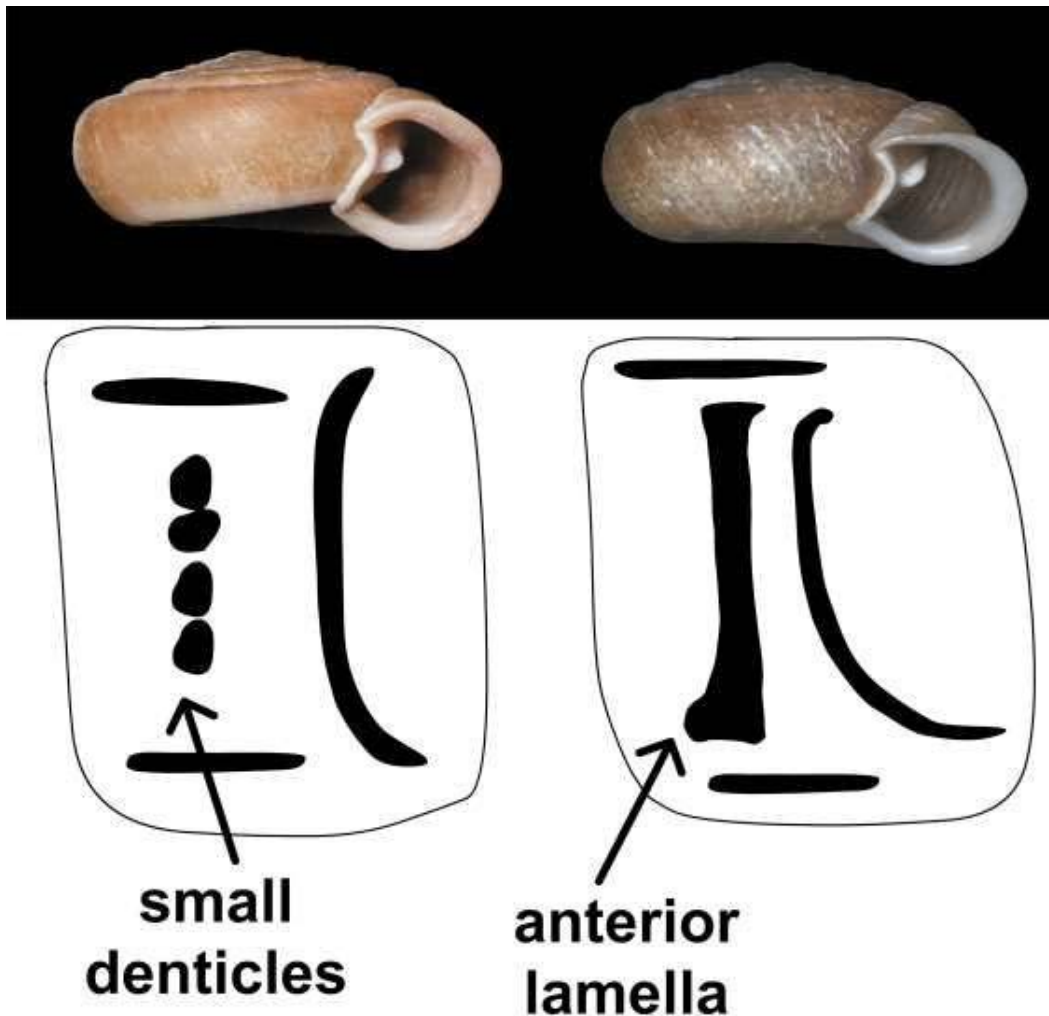


Figure 8.19. Two types of a single species *Gudeodiscus phlyarius* collected from adjacent localities in the vicinity of Duan city, Guangxi, China.

The shells showed on Figure 9.19 did not discretely differ in shape, spire height, sculpture or aperture shape. However, they differed in anterior lamella present in the right specimen, and small denticles present in the left specimen.

Similarly in Northern Vietnam, specimens of *Gudeodiscus fischeri* had an anterior lamella, but other specimens from a near place had small denticles instead of anterior lamella. Moreover, these character states were found in specimens of *Gudeodiscus messengeri raheemi* u. ssp. from the same locality.

These three cases suggest that the denticles anterior to the single lamella ("C") and the anterior lamella ("E") are variable phenotypes within single species and thus probably represent homologous characters.

(2) The denticles in character state "G" are homologous with the posterior lamella in character state "E".

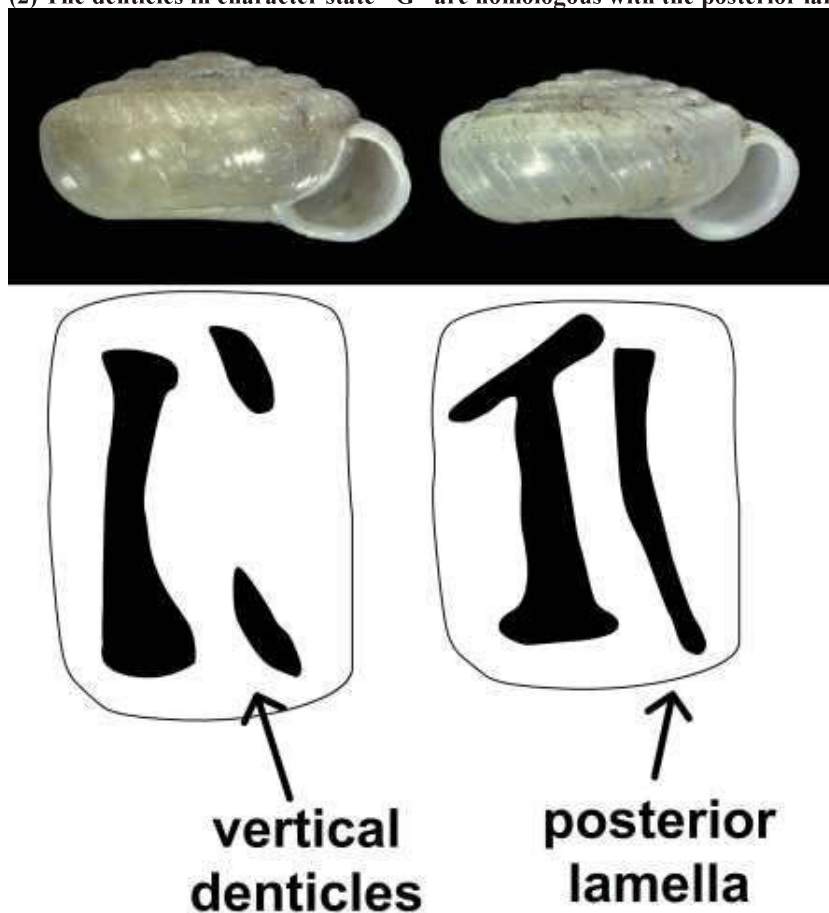


Figure 8.20. shells and parietal plication of *Sicradiscus cutisculptus* (left) and *S. diptychia*.

Most *Sicradiscus* species have "E"-type lamellation with an anterior lamella and a slender, curved posterior lamella such as the right specimen of *Sicradiscus diptychia*. The left specimen (Figure 8.20) of *Sicradiscus cutisculptus* was similar to the right specimen of *S. diptychia* (Figure 8.20) in shell characters (general shell and aperture shape, sculpture, and morphology of palatal plicae). Their main difference is in the presence of a posterior lamella in *S. diptychia* and the presence of two vertical denticles in *S. cutisculptus*. The vertical denticles in the latter are found in the position of the posterior lamella of the former species. This suggests that these traits are homologous.

Most species of the genus *Endothyrella* have one or two small denticles posterior to the lamella. Because of their closely similar locations, I assume that the denticles in *Endothyrella* are also homologous with the posterior lamella of the character state "E".

(3) In Tribe2 the two lamellae type ("E") is ancestral, and the others are derived.

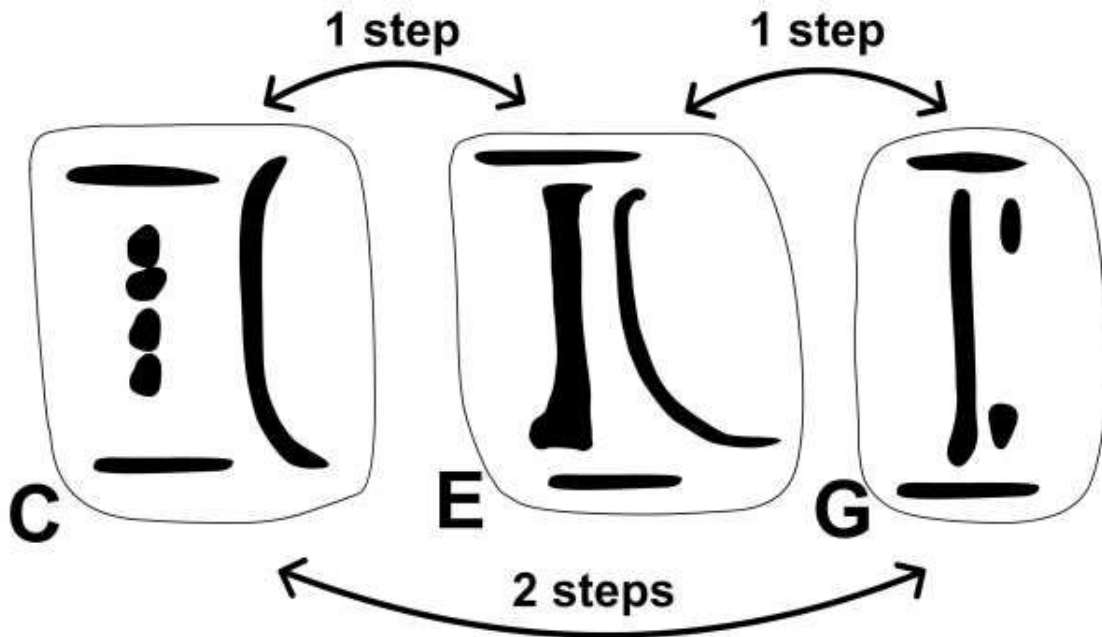


Figure 8.21. Both the character states "C" and "G" can be derived from the double lamellae-type ("E") by the reduction of one of the lamellae, namely the anterior lamella in case of "C", and the posterior lamella in case of "G" (see assumptions 1 and 2). Also, the character state "G" cannot be derived logically from "C" without the character state "E". This suggests that the ancestral character state in Tribe2 is the one with two lamellae ("E").

(4) The single lamella in the character state "B" is homologous with the posterior lamella in "C".

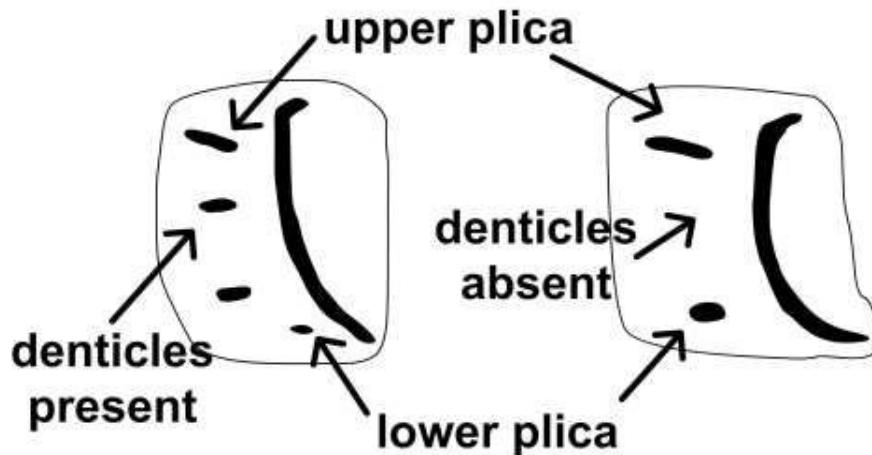


Figure 8.22. Parietal lamellation of two specimens of *Gudeodiscus eroessi eroessi* (locality 2009/74). The left specimen had four denticles and the right specimen two denticles. The lowermost plica represents the lower plica, and the uppermost plica represents the upper plica in both cases. However, the left specimen has two small denticles between the upper and lower plicae, whereas the right specimen lacks them.

Similarly to the case depicted on Figure 8.22, either "B" or "C"-type plication were found in neighbouring populations of the species *Gudeodiscus multispira* and *Sinicola reserata azona* (see Páll-Gergely & Hunyadi 2013).

My assumption is that the "B"-type is derived from the "C"-type by the further reduction (disappearance) of the anterior lamella. The character state lacking the anterior lamella ("B") might have been developed by the gradual reduction of the anterior lamella (character state "E" through character state "C"), or directly from character state "E". The other possible direction, namely that the E-type is developed from the B-type having the transitional character state C-type is less probable, because the E-type is assumed to be the ancestral character state in the Tribe2 (see previous assumption).

(5) The upper and lower plicae can be absent in the genus *Gudeodiscus*. As a result, only a single, curved lamella is visible.

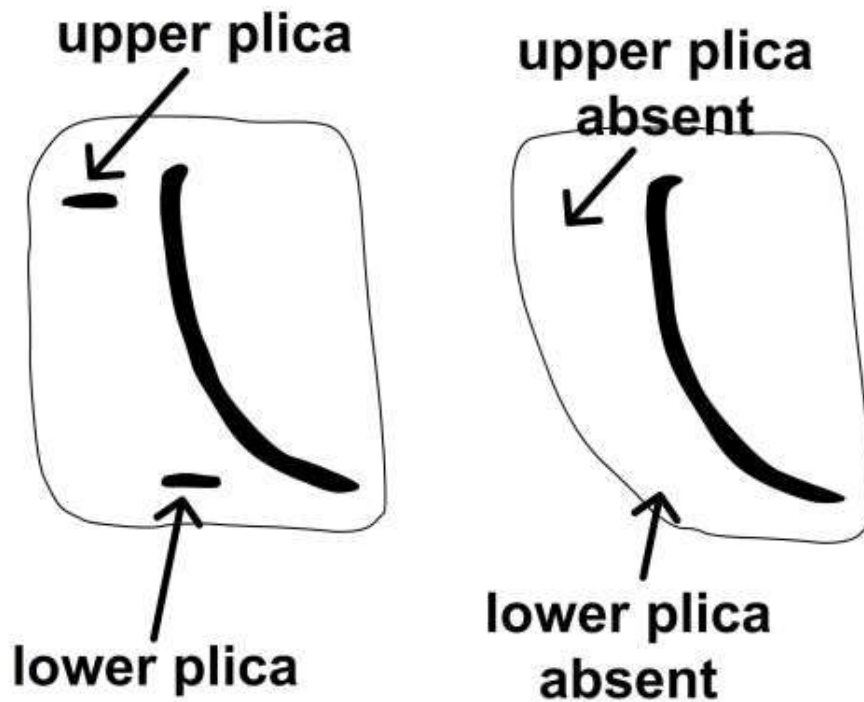


Figure 8.23. *Gudeodiscus pulvinaris robustus* specimens from different populations.

In some populations of *Gudeodiscus pulvinaris robustus*, there is only a single, curved parietal lamella. The figure on the right shows a specimen from a populations near Xinanshe. Other populations of the same taxon having identical shells characters (shell, aperture shape, palatal plicae, apertural fold, etc.) have two horizontal plicae anterior to the lamella (figure on the left, specimen from Lianggu Cun). This suggests that the single lamella in some populations of this taxon is homologous with the posterior lamella of the two lamella-type ("E"), as assumed for the character states "B" and "C".

(6) The single lamella in *Endothyrella* (character state "H") and *Gudeodiscus* (character state "A") are probably of different origin.

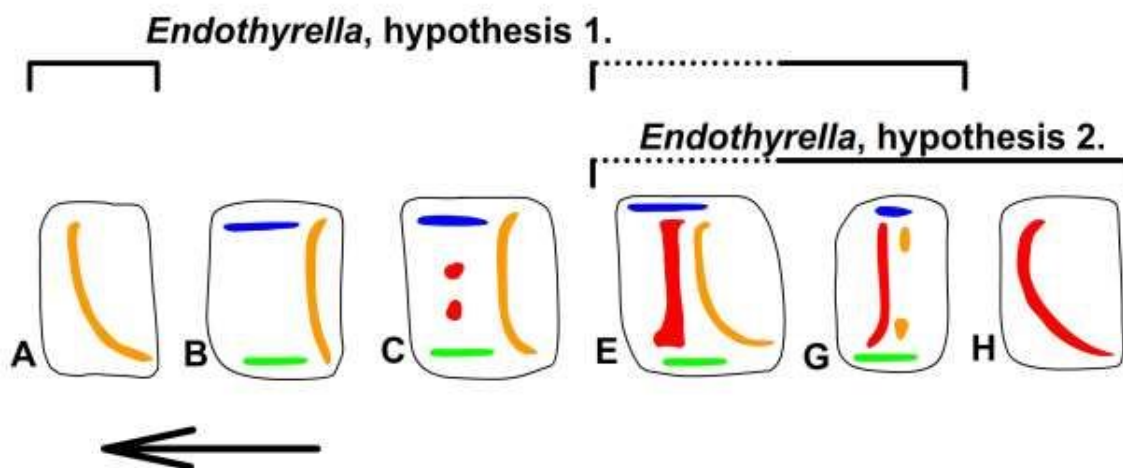


Figure 8.24. Two hypotheses explaining the origin of the character "H" in the genus *Endothyrella*.

In the genus *Gudeodiscus* we can find specimens which has only a single curved lamella. My assumption is that this lamella is homologous with the posterior lamella of the character state "E" (see previous assumption). In two species of the genus *Endothyrella* (*E. babbagei* and *E. species6 u. sp.*) we can also find single, curved lamellae without additional denticles or plicae ("H"). These single lamellae are similar to the single lamellae of some *Gudeodiscus* specimens. The origin of the single lamella in *Endothyrella* can be explained by two hypotheses:

First hypothesis: The single lamella in *Endothyrella* represents the posterior lamella of the character state "E".
Second hypothesis: The single lamella in *Endothyrella* represents the anterior lamella of the character state "E".

My assumption is that the second hypothesis is more probable. This assumption is only based on the observation that most *Endothyrella* species have the posterior lamella dissolved into small denticles (see assumption 2).

In the genus *Gudeodiscus* the anterior lamella is usually straight and the posterior is curved (Figure 3E). My hypothesis is that in face of the curved shape of the single lamella in two *Endothyrella* species represents the anterior lamella. This hypothesis is supported by the fact that the single lamella of *Endothyrella williamsoni* (Fig. 3I) is also curved, but I assume its homology with the anterior lamella instead of the posterior lamella because of the presence of posterior denticle (see assumption 2).

(7) The middle horizontal parallel plicae (character state "D") anterior to the lamella of character state "E" are homologous with the remains of the anterior lamella.

In the taxa *Gudeodiscus emigrans quadrilamellatus* and *Sinicola reserata hensanensis* (Yen 1939), and in some specimens of *G. emigrans otanii* and *Sinicola schmackeri* there are four, approximately equally long parallel plicae anterior to the single curved lamella. *Gudeodiscus ursula* Páll-Gergely & Hunyadi 2013 has six plicae anterior to the lamella, the first and last being conspicuously longer than the four in the middle. I assume that the uppermost and the lowermost plicae which run close to the upper and lower sutures, are homologous with the upper and lower plicae of other plectopylid species (see assumptions 8 and 9). The origin of the horizontal middle plicae can be explained by two probably different ways:

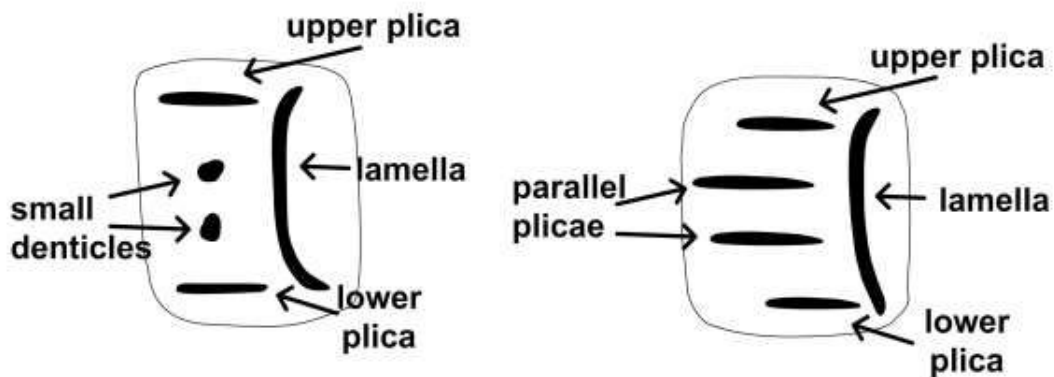


Figure 8.25. **First hypothesis:** *Gudeodiscus ursula* is very similar in shell shape to *G. multispira*. The plicae on the parietal wall are also similar, but *G. ursula* has elongated middle plicae. My assumption is that the middle plicae have been developed by the elongation of separate denticles (see Fig 3C). The same relationship is assumed in case of the small denticles of *Sinicola reserata azona* (left image) and the long parallel plicae of *Sinicola reserata hensanensis* (right image).

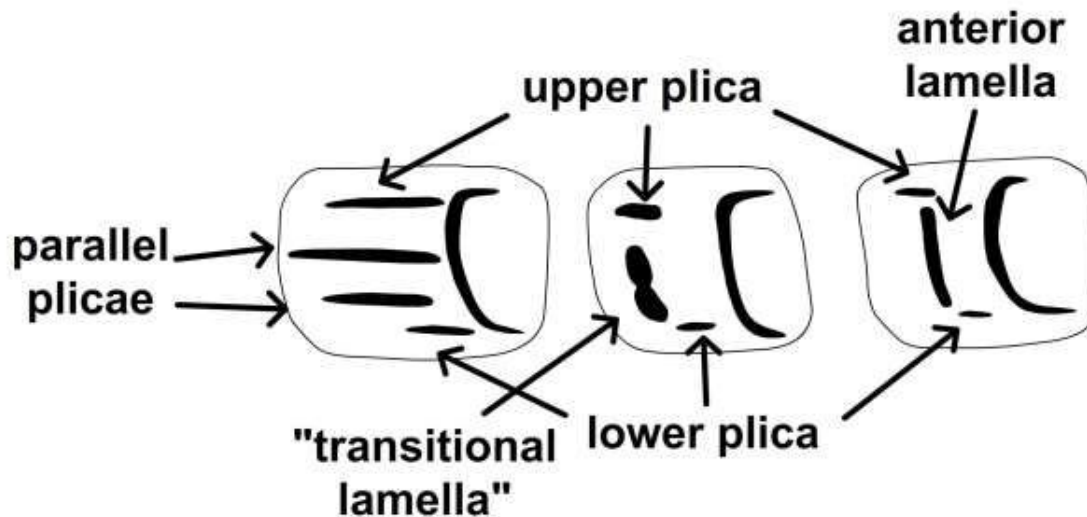


Figure 8.26. **Second hypothesis:** In the same population of *Gudeodiscus emigrans otanii* specimens with both "D"-type (image on the left) and "E"-type (image on the right) lamellation were found (Páll-Gergely & Hunyadi 2013, Páll-Gergely & Asami 2014). Moreover, a shell with intermediate character state was also reported (image on the middle, Páll-Gergely & Asami 2014). I assume that the middle parallel plicae of *G. emigrans otanii* and *G. emigrans quadrilamellatus* were possibly developed "directly" from the anterior lamella by its fragmentation into two portions and by the turn of both fragments into anterior-posterior direction. In this hypothesis the character state "C" (small denticles anterior to the posterior lamella) is missing.

(8) The single lamella in *Chersaecia* represents the posterior lamella.

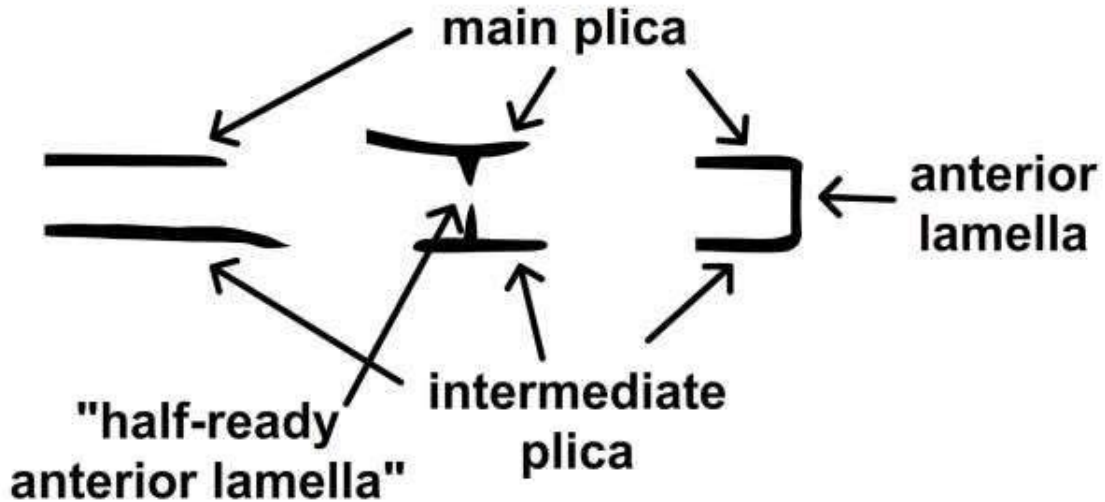


Figure 8.27. This figure shows the main and intermediate plicae and the anterior lamella only, the posterior lamella and the lower plica are not shown. *Chersaecia* (sensu Gude 1899e) species have one lamella (character state "J"; image on the left), whereas *Plectopylis* (sensu Gude 1899e) have two (character state "L"; image on the right). In one specimen of *Character perrierae* (2009.10.19A) there was a slight lime layer which formed a "half-ready" vertical lamella similar to the anterior lamella of *Plectopylis* species and on the same relative position (character state "B" and figure in the middle).

Addition to the case on figure 8.27, *Chersaecia leiophis* (one lamella) and "*Plectopylis*" *goniobathmos* (two lamellae) are similar in all shell characters except for the presence/absence of an anterior lamella. These information suggest that the single lamella of *Chersaecia* is homologous with the posterior lamella of *Plectopylis*.

(9) In Tribe1 the one-lamella-type (character state "A") is ancestral, and the two lamellae type (character states "C"–"D") is derived.

The probably most basal group of Plectopylidae, the genus Genus1 has only one lamella, which suggests that it is the ancestral character state in Plectopylidae.

(10) The lower plicae close to the lower suture is homologous in all Plectopylidae species.

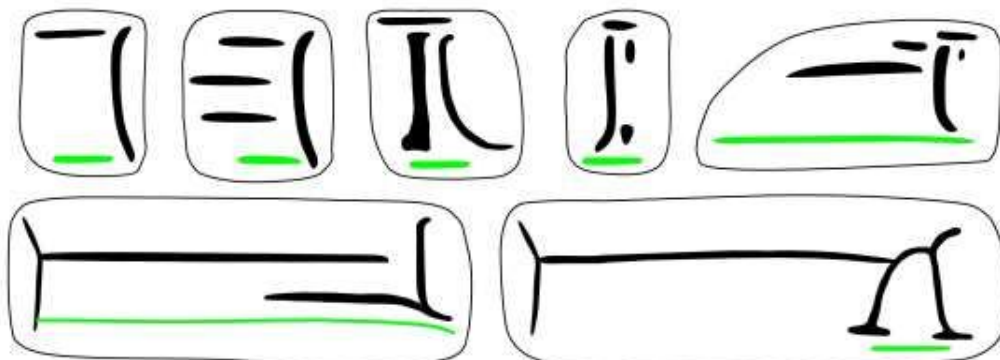


Figure 8.28. Lower plicae (green) of different taxa of Plectopylidae.

In most species of Plectopylidae a plica is visible under the anterior lamella, very close to the lower suture. In some genera (*Chersaecia*, *Plectopylis* and *Endothyrella*) this plica can be long and reach the peristome, or can be short. In other genera (*Endoplon*, *Sinicola*, *Gudeodiscus*, *Sicradiscus*) however, only short lower plica is known. The position of this plica is identical in all cases (indicated by green colour in the image). Therefore I assume that the lower plica is homologous in all species of the Plectopylidae.

(11) The lower plica of *Gudeodiscus villedaryi* (character state "F") is of unknown homology.

Gudeodiscus villedaryi has an anterior lamella which possesses anteriorly as well as posteriorly elongated lower end, and a free horizontal plica close to the lower suture (Character state "F"). The formation of this character state can be explained by two hypothesis:

Hypothesis 1:

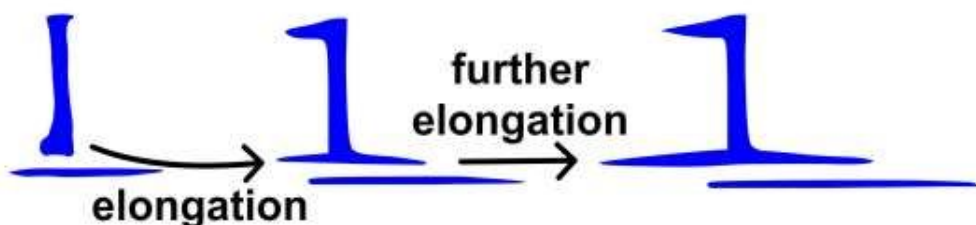


Figure 8.29. **First hypothesis:** The lower end of the anterior lamella has been elongated both in anterior and posterior directions, and the plica under the anterior lamella is the lower plica, which is homologous with that of the other *Gudeodiscus* species.

The figure above shows the anterior lamella and the lower plica only. The first image corresponds to the character state "E", and the last image with the character state "F". The image in the middle is a hypothetical intermediate form.

Hypothesis 2:

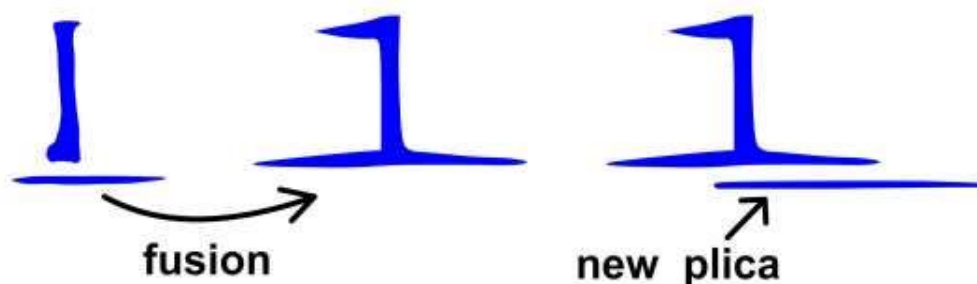


Figure 8.30. **Second hypothesis:** the anteriorly and posteriorly elongated lower end of the anterior lamella had been developed by the fusion of the anterior lamella and the lower lamella, and the additional plica below this complex (very close to the lower suture) is a secondary plica, which is not homologous with the lower plica of other *Gudeodiscus* species.

The figure above shows the anterior lamella and the lower plica only. The first image corresponds to the character state "E", and the last image with the character state "F". The image in the middle is a hypothetical intermediate form.

(12) The upper plica close to the upper suture is homologous in all Tribe2 species.

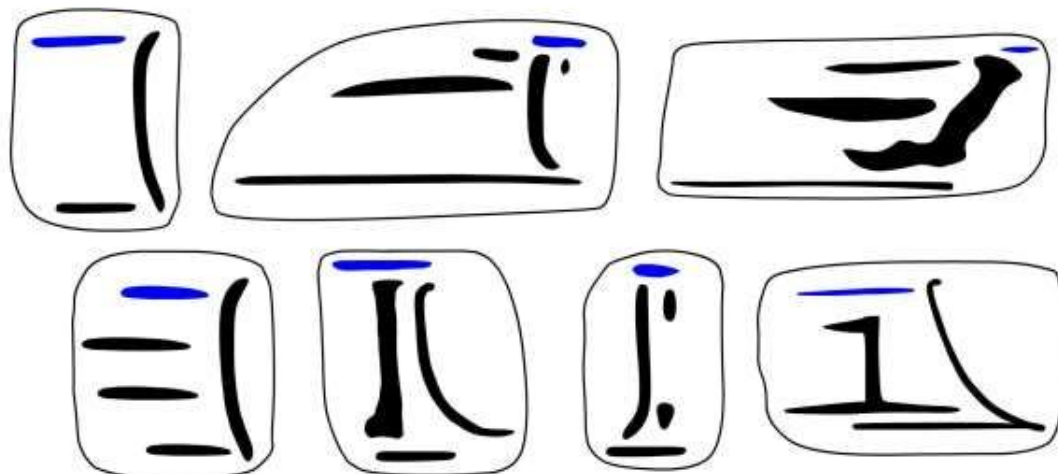


Figure 8.31. Upper parietal plica (blue) of different species of Tribe2.

In most species of Tribe2 a plica is visible above the anterior lamella, very close to the upper suture. No upper plica has been found in species of Tribe1 and Subfamily1. The position of this plica is similar in all cases, namely above the anterior plica, or the position of the anterior plica, when it is missing. Therefore I assume that the upper plica is homologous in all species of the Plectopylidae.

(13) One of the horizontal plicae anterior to the lamella in *Endothyrella* (character state "I") is homologous with the main plica of *Plectopylis* and *Chersaecia*, but it is not homologous with any of the middle horizontal plicae in *Gudeodiscus* and *Sinicola*. The other horizontal plica of *Endothyrella* is without homologous structure in the family.

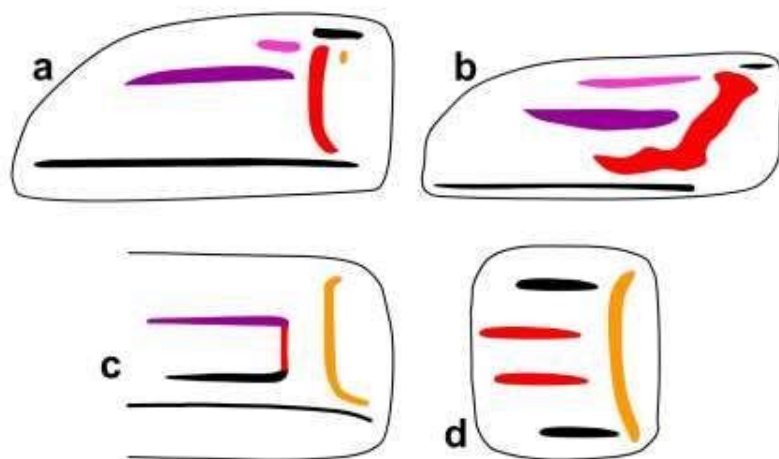


Figure 8.32. In this picture purple indicates the main plica, mustard yellow the posterior lamella (and homologous structures), red the anterior lamella (and homologous structures), and pink the "additional" horizontal plica. A: *Endothyrella williamsoni*; B: *Endothyrella brahma*; C: *Chersaecia* sp.; D: *Sinicola/Gudeodiscus* sp.

In two *Endothyrella* species (*E. brahma* and *E. williamsoni*) there are two horizontal plicae anterior to the lamella. The lower one, which is thicker and longer than the other is probably homologous with the main plica of *Plectopylis* and *Chersaecia* because of the similar relative position of these plicae (Figure "I"). The other horizontal parietal plica which is situated above the main plica, however, probably has no homologous structure in other Plectopylidae species.

The single lamella in *Endothyrella* (character state "I") is probably homologous with the anterior lamella of the character state "E" (see assumption 2). However, the lamella of *Gudeodiscus* and *Sinicola* species having "D"-type lamellation is homologous with the posterior lamella of the character state "E" (see assumption 1). The parallel horizontal plicae of character state "D" are homologous with the anterior lamella of character state "E". Based on these information, my assumption is that the main plica in *Endothyrella* are not homologous with any of the horizontal plicae of *Gudeodiscus* and *Sinicola*.

(14) The apertural fold and the main plica are of different origin.

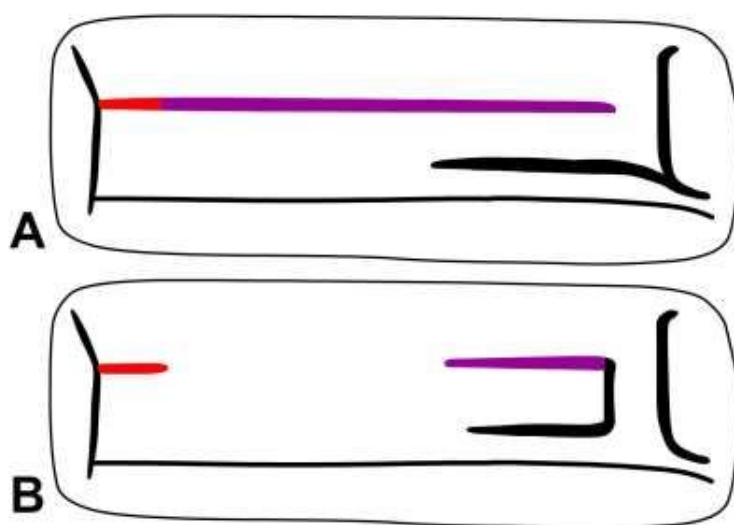


Figure 8.33. The majority of species in the genera *Plectopylis* and *Chersaecia*, and some *Endothyrella* species possess a long, horizontal, main plica (character states "I", "J"–"M"), which is situated in approximately the middle of the parietal wall, somewhat closer to the upper suture. Usually, this plica reaches the aperture margin without interruption in the genera *Plectopylis* and *Chersaecia* (Figure 8.33A). In *Endothyrella* the main plica does not reach the peristome. In some species of *Plectopylis* and *Chersaecia* however, this long plica is entirely missing or reduced to short (Figure 8.33B). Even in those species without or with short main plica, there is a short apertural fold. This information suggests that these two structures, namely the apertural fold (indicated by red) and the main plica (indicated by purple) are of different origin and has to be handled as two independent structures.

In the family Clausiliidae the superior lamella is situated in the same relative position as the plectopylid apertural fold, and clausiliid spiral lamella is in the same relative position as the plectopylid main plica. In most clausiliid species the two lamellae are in contact with each other, but in a few species they do not reach each other, but passes next to each other. Even in species with joined spiral and superior lamellae they are formed independently during development and they reach each other after both are nearly complete (Páll-Gergely 2010 and references therein).

(15) The short lower parietal plica and the absence of the main plica are apomorphic characters.

See in Discussion under apomorphic and plesiomorphic characters.

Chapter 9a: Discussion: Apomorphic and plesiomorphic characters

During the identification of plesiomorphic (ancestral) and apomorphic (derived) characters, I was largely relying on the characters of Genus1 *dextrorsa*, which I consider as the most basal (ancient) lineage of the family Plectopylidae. The family Corillidae has been accepted as the closest relative of Plectopylidae ("outgroup").

The anatomy of Genus1 *dextrorsa* differs largely from that of the other plectopylid species (see under that species in Chapter 7). At the moment it is not possible to decide whether all of the features represent plesiomorphic characters, or some of them are autapomorphic characters of Genus1 *dextrorsa*. For sake of simplicity I handle the anatomical features of Genus1 *dextrorsa* as plesiomorphic characters of Plectopylidae.

Coiling direction: Both Genus1 *dextrorsa* and the family Corillidae are dextral, therefore I assume that the original coiling direction of the family Plectopylidae was also dextral.

Presence of the apertural fold: Both Genus1 *dextrorsa* and the family Corillidae possess an apertural fold. Moreover, in nearly all genera, with the exception of *Endothyrella* we can find species having apertural fold. This suggests that the presence of the apertural fold is plesiomorphic, and the lack of it is apomorphic.

Presence/length of the main plica: Both Genus1 *dextrorsa* and most species of the family Corillidae has a long main plica, which is connected to the apertural fold (they form a continuous plica until the peristome). This suggests that the long main plica is plesiomorphic and the short or missing main plica is apomorphic.

Presence/length of the lower plica: Genus1 and *Corilla* lack a lower plica, which suggests that the absence of the lower plica is plesiomorphic and the presence is apomorphic. The long lower plica, which reaches the peristome is probably plesiomorphic character in Subfamily2, whereas the short lower plica, which is present only under the anterior lamella or in respective position, is apomorphic. This assumption is based on first, the hypotheses that most character states of *Plectopylis* and *Chersaecia* (with usually long lower plica) are probably plesiomorphic, and second, on the assumption that the lower plica was reduced together with the main plica.

Number of lamellae: Genus1 *dextrorsa* has a single lamella. In the genus *Chersaecia* we can find species with a single, and other with two lamellae. Moreover, there are even intermediate forms between the single and double lamella-type. This suggests that the presence of a single lamella is plesiomorphic in the family Plectopylidae, whereas the presence of two lamellae is apomorphic. However, within the tribe Tribe2 the single lamella is probably a result of secondary reduction, and the presence of two lamellae is ancestral. See also in Chapter 8.

Presence of periostracal folds standing in spiral lines: Genus1 *dextrorsa* has flat, relatively large periostracal folds standing in a single row on the blunt keel of the body whorl. Very similar folds are visible in *Plectopylis* species2 u. sp. and in most *Sinicola* species. This indicates that this is a plesiomorphic character which remained in some of the distantly related taxa. Corillidae has no periostracal folds, which may mean that the folds are synapomorphies of Plectopylidae. The absence of the periostracal folds and the presence of folds standing in multiple spiral rows are considered apomorphic.

Sculpture of the protoconch: Both Genus1 *dextrorsa* and all species of the Corillidae possess smooth protoconch. This smooth or finely tuberculated protoconch is widespread in the genera *Endoplion*, *Plectopylis* and *Chersaecia*. These indicate that the finely, regularly ribbed protoconch of Tribe2 is apomorphic, whereas the smooth or tuberculated protoconch is plesiomorphic. In some species of Tribe2 (e.g. *Endothyrella* species6, *Gudeodiscus villedaryi*) the protoconch is smooth. This is probably the result of secondary reduction.

Spire height: Both Genus1 *dextrorsa* and the species of the family Corillidae are almost entirely flat. This trait is visible in all *Plectopylis*, *Endoplion* and *Chersaecia* species. Therefore, the flat shell is considered as ancestral and the elevated spire as derived. Some species of *Endothyrella* and *Gudeodiscus* have elevated spire which is associated with a narrow umbilicus.

Size of the central tooth in relation to the ectocone of the first lateral tooth: Genus1 *dextrorsa*, *Plectopylis*, *Chersaecia*, *Halongella* and *Gudeodiscus* (*Veludiscus*) have smaller central tooth than the ectocone of the first laterals. The genera *Sicradiscus*, *Gudeodiscus* (*Gudeodiscus*), *Sinicola* and *Endothyrella* have in general as large central tooth as the ectocone of the first lateral tooth, or even larger. These information indicate that the small central tooth is a plesiomorphic character.

Morphology of the marginal teeth: The tricuspid marginal teeth with pointed cusps and the presence of deep incision between the innermost cusps is in strong association with the large central tooth. In contrast, the bicuspid marginals, or tricuspid marginals with blunt inner cusp and shallow incision between the innermost cusps occurs in the groups which have small central tooth. This suggests that the presence of tricuspid marginal teeth with sharp cusps is a derived character.

Sculpture of the inner wall of the penis: Genus1 *dextrorsa* has a thick-walled penis with longitudinal folds on the inner wall. All other Plectopylidae have more or less parallel folds on the inner penial wall, which is probably a synapomorphy of Plectopylidae. The presence of determined pockets standing in one or two rows on the inner penial surface is characteristic for all *Gudeodiscus* and some *Sicradiscus* species, and probably a synapomorphy of those genera.

Presence of an epiphallus: Genus1 *dextrorsa* has a penis-epiphallus-vas deferens complex, which is a thick-walled tube of the same thickness from its beginning to its end. None of these organs are discernible by looking. All other Plectopylidae species has a well distinguishable penis, epiphallus and vas deferens, with the exception of Genus3 *laomontana* and two *Chersaecia* taxa (*perarcta simplex* and *perrieriae*). In those species the epiphallus is not visible, and the vas deferens starts from the proximal end of the penis. This reduction of the epiphallus may be autapomorphy of some species, and the presence of an epiphallus is probably a plesiomorphic character.

Presence of a penial caecum: Genus1 *dextrorsa* lacks a penial caecum and *Chersaecia* and *Plectopylis* also has no, or very small penial caecum. Most species of Tribe2 has a penial caecum, but some of them lack it. It seems that the presence of a penial caecum is an apomorphic character, but the absence in Tribe2 can be results of secondary reductions.

Presence of a penial retractor muscle: Genus1 *dextrorsa* lacks a penial muscle, which is present in all other plectopylid species. The presence of a retractor muscle can be an apomorphic character, or the absence of the muscle is an autapomorphy of Genus1 *dextrorsa*.

Presence of the diverticulum: When the absence of the diverticulum is reported in some species of Tribe2, it is difficult to exclude the possibility that it was simply overlooked (see under remarks on the anatomy). If the diverticulum is really absent, that might be due to secondary reduction, because all anatomically known *Plectopylis* species, the genus Genus1, and most species of Tribe2 possess a diverticulum.

Size of the diverticulum: Genus1 *dextrorsa* has a diverticulum which is considerably shorter than the bursa copulatrix. This is often the case in the genera *Plectopylis* and *Chersaecia*, which are characterized by several symplesiomorphic characters. These data suggest that the short diverticulum is a plesiomorphic character, whereas a long one (as long as the bursa copulatrix) is an apomorphic character.

Presence and morphology of calcareous granules within the penial lumen: Some *Gudeodiscus* species have claw or hook-like calcareous crystals within the pockets formed by longitudinal folds on the inner penial surface. *Halongella schlumbergeri* has T-shaped, flat calcareous granules between its penial folds. In some *Sinicola* and *Endothyrella* species rounded or flat calcareous granules have been found. No calcareous granules were found in the penis of *Plectopylis* and *Chersaecia* species, but this may be due to the small number of specimen dissected. The granules are probably strongly associated with the mating period of the snails and therefore, they are rare. Moreover, some of these granules may be "half ready", which should be taken into account during the analysis of the taxonomic significance of their shape. At the moment I have not enough information to refer to the evolutionary significance of the calcareous granules, and to hypothesize the shape of ancestral granules.

Chapter 9b: Discussion: Taxonomic relationships of the genera of Plectopylidae

Genus1

Genus1 *dextrorsa* is separated into its own subfamily (Subfamily1) because of the very radical differences in its anatomy in relation to all of the plectopylid taxa. The ommatophoral retractor of Genus1 does not run between the penis and the vagina, but passes along these organs. There is a small, blindly-ended organ with its own retractor muscle which has not been found in any other member of Plectopylidae. Retractor muscle of the penis was not found in Genus1, but it is present in all other plectopylid taxa. Moreover, the penis-epiphallus-vas deferens tube does not show any signs of diversification. It is equally thick from the atrium until the insertion to the female part. These anatomical differences, although maybe not all of them, likely represent ancient traits, not autapomorphic characters.

Tribe1

The subfamily Subfamily2 is divided into two tribes, namely Tribe1 (*Chersaecia*, *Endoplion* and *Plectopylis*) and Tribe2 (Genus2 u. gen., *Endothyrella*, *Gudeodiscus*, *Halongella*, Genus3 u. gen., *Sicradiscus* and *Sinicola*). Tribe1 is characterized by a smooth but matt or tuberculated protoconch and the presence of long main and lower plicae which usually reach the peristome, whereas Tribe2 possesses a finely ribbed protoconch and usually lacks long main and lower plicae. I have not found clear distinguishing anatomical character between the two tribes, but there are some differences which are characteristic of one of the tribes only. These differences are the following: (1) Calcareous granules are frequently found in species of Tribe2, but no calcareous granules have been found in the penis lumen of

Tribe1 species. This, however, can be due to the low number of examined specimen only. (2) Well-developed penial caeca are usually present in Tribe2, but in Tribe1, even if present, they are vestigial. (3) The bursa copulatrix and the diverticulum (when present) are always mostly of the same size in Tribe2, but in Tribe1 the diverticulum is usually shorter than the bursa copulatrix.

Plectopylis* and *Chersaecia

The genus *Chersaecia* has more diverse palatal and parietal fold system than *Plectopylis*. Namely, the single- or double lamellae-type are also present in *Chersaecia*, whereas all *Plectopylis* species have two lamellae which are fused at their upper ends. The palatal plicae of some *Chersaecia* species are horizontal, in others, however, the 4th and 5th plicae are fused and form a vertical plate, similar to that of *Plectopylis*. In the genus *Plectopylis* only the latter type of palatal plication is present. Moreover, limited information on their anatomy suggests that the reproductive system in *Chersaecia* is more diverse than that of *Plectopylis*, because the epiphallus is missing in some *Chersaecia* species, but present in others. On the other hand, all species of *Plectopylis* which are known anatomically possess a well differentiated epiphallus. These data suggest that *Plectopylis* is probably monophyletic because of the uniformed shell characters throughout the genus. *Chersaecia* however, may be paraphyletic without *Plectopylis*, because all characteristic features of *Plectopylis* are present in some taxa of *Chersaecia*, except for the fused lamellae.

Endoplion

The genus *Endoplion* has a robust shell, similar to that of *Plectopylis*. The plicae on the other hand, are similar to the genus *Chersaecia*. Very few shell specimens are known of the two *Endoplion* species, and no freshly collected specimens are available for anatomic study. Therefore, the systematic position of the genus *Endoplion* is not clarified yet. *Endoplion* may belong to Subfamily1 or to Subfamily2. The latter is more probable because Genus1 has well-developed periostracal filaments, which are missing in *Endoplion*. *Endoplion* is dextral, whereas both genera of the Tribe1 (*Plectopylis* and *Chersaecia*) are sinistral. Therefore, the most parsimonious hypothesis is that *Endoplion* branched off before *Plectopylis* and *Chersaecia*, namely when the coiling direction changed from dextrality to sinistrality.

Genus2

The tribe Tribe2 consists of the genera *Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola*, *Endothyrella*, Genus3 u. gen. and Genus2 u. gen. All of these genera possess fine radial ribs on their embryonic whorls. The anatomy of the two species belonging to Genus2 u. gen. is unknown, therefore no extensive discussion on their taxonomic position is possible. The characteristic feature of that genus is the presence of spiral sculpture along with the radial ribs on the protoconch, resulting in a reticulated sculpture. All other genera possess ribbed protoconch. One *Endothyrella* species, *E. serica* has a spiral line running close to and parallel with the suture. The taxonomic significance of this trait is unknown. This single spiral lines is probably not homologous with the spiral sculpture of Genus2 u. gen. species, and can be interpreted as the autapomorphy of *Endothyrella serica*. Genus2 species3 u. sp. has about 12 spiral lines on its protoconch, whereas *Genus2 andersoni* has approx. six lines. In both species these spiral lines are situated about equidistantly from each other and cover the whole protoconch.

Because of the unique, regularly spirally striated protoconch the genus is hypothesized as the most basal group of the Tribe2.

Genus3

Genus3 *laomontana* is the only species belonging to its genus. It is characterized by a protoconch covered with wavy, dense riblets. The ribs on the protoconch of other genera (*Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola*, *Endothyrella*) are straight and have wider space between them. Genus3 *laomontana* lacks an epiphallus which is present in all other taxa in Tribe2. In the genus *Chersaecia* (tribe Tribe1) the epiphallus is absent in two species (*perarcta simplex*, *perrierae*), whereas a third species (*shanensis*), which is similar in shell characters to the previous two, has a well-differentiated epiphallus. The epiphallus has probably been reduced independently in the two tribes. Addition to the conchological differences between Genus3 and *Chersaecia*, this hypothesis is supported by the different position of the vas deferens in the two groups. In case of the two *Chersaecia* species the vas deferens is first recognisable near the proximal part of the penis, whereas in Genus3 *laomontana* it becomes an independent organ at the middle section of the vagina.

Because of the lack of the epiphallus, the dense, wavy ribs on the protoconch and the radula showing plesiomorphic characters, Genus3 is hypothesized to be the sister group of the clade containing *Halongella*, *Gudeodiscus*, *Sicradiscus*, *Sinicola* and *Endothyrella*.

Endothyrella*, *Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola

The genera *Endothyrella*, *Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola* share the regularly ribbed protoconch and the presence of an epiphallus. Some *Endothyrella* and *Sicradiscus* species, *Gudeodiscus villedaryi* and *G. dautzenbergi*, however, possesses rather smooth protoconch. In these species the ribs are completely absent, or present only near the suture or at the end of the embryonic whorls. These, rather smooth protoconchs can be explained by secondary reduction, because the above-mentioned species are conchologically and anatomically similar to other species possessing ribbed protoconchs.

Endothyrella

The genera of Tribe1 (*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. The main plicae and the lower plicae of *Endothyrella* and Tribe1 are probably homologous, respectively. The presence of these long plicae in *Endothyrella* might be symplesiomorphic characters of *Endothyrella*. *Endothyrella* has similar, probably apomorphic radula features to *Gudeodiscus* (*Gudeodiscus*) and *Sinicola*. Namely, the central tooth is as large as or larger than the ectocone of the first laterals, and the marginals are tricuspid with deep incision between the cusps. The presence of a penial caecum and calcareous hooks on the inner wall of the penis are also apomorphic characters. Because of the plesiomorphic shell and the apomorphic radula and genital characters the systematic position of *Endothyrella* is questionable. Moreover, the geographic distribution of *Endothyrella* and *Chersaecia* overlaps, which can support their common origin. In face of the long main and lower plicae, here I refer to *Endothyrella* as a close relative of *Sinicola* and *Gudeodiscus* because of the similar radula, the presence of a penial caecum and calcareous hook-like granules inside the penis. The long horizontal plicae are hypothesized to be the results of secondary elongation.

Endothyrella* and *Sicradiscus

The genus *Sicradiscus* seems to be the closest relative of *Endothyrella* because of the weak or sometimes reduced posterior lamella. Moreover, juvenile specimens of *Sicradiscus transitus* have hairs standing in two spiral lines on the body whorl. The homology of the hairs standing in spiral lines in *S. transitus* and in *Endothyrella* is, however, questionable. In *Endothyrella* the hairs are arranged in 3–7 spiral lines, whereas in *S. transitus* they are standing only in two rows. This trait seems to be absent in adult *S. transitus* shells and all other species of *Sicradiscus*, but common in fully grown *Endothyrella* shells. The two genera (i.e. *Endothyrella* and *Sicradiscus*) differ in the short, straight palatal plicae which are usually connected in *Sicradiscus* and longer, more complex palatal plicae sometimes having additional denticles in *Endothyrella*. In both genera divided plica may occur, but in case of *Sicradiscus* the posterior fourth and fifth plica seems to be always connected, whereas in *Endothyrella* all plicae are free. Moreover, "western" *Sicradiscus* species (*feheri*, *invius*, *mansuyi*, *securus* and *transitus*) differ from *Endothyrella* by the presence of a strong apertural fold.

Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola

The genera *Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola* share the absence of long main and lower plicae. 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. My investigations on the reproductive anatomy 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. The genus *Gudeodiscus* is divided into two subgenera based on the morphology of the distal penis-penial caecum-retractor muscle complex. In the subgenus *Veludiscus*, 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 subgenus *Gudeodiscus* the epiphallus has a somewhat thickened proximal part, and has no additional muscle fibres attached to the penis.

Plectopylis schlumbergeri and *P. fruhstorferi* are conchologically indistinguishable from *Gudeodiscus* species, but had only parallel folds on the inner penial wall without pockets. Based on this morphological character, they are moved to a new genus, *Halongella*. *Halongella* is hypothesized as the sister group of the clade including the genera *Gudeodiscus*, *Sinicola*, *Sicradiscus* and *Endothyrella* because of the plesiomorphic traits of its radula and the lack of the penial caecum, which is present in most species of the other four genera.

The taxonomic position of the species classified within *Sicradiscus* is problematic. The genus *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 keeled 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 similarly to that of *S. feheri*. Moreover, *S. transitus* ranges between *S. feheri* and *S. schistoptychia* geographically. The inner morphology of the penis in *S. schistoptychia*, however, 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. 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, my 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*. Species of *Sicradiscus* may not be monophyletic, but *Sinicola* and *Gudeodiscus* probably are.

Chapter 9c: Discussion: Taxonomic changes

New taxa

Based on anatomical information, I propose to subdivide the family to two subfamilies, Subfamily1 u. subfam. and Subfamily2 u. subfam. I propose the subdivision of the latter subfamily into two tribes (Tribe1 u. trib. and Tribe2 u. trib.) based on mainly conchological traits. The following genera and subgenera are proposed as new to science:

Genus1 u. gen.

Genus2 u. gen.

Gudeodiscus Páll-Gergely 2013,

Gudeodiscus (Veludiscus) Páll-Gergely 2015

Halongella Páll-Gergely 2015

Genus3 u. gen.

Sicradiscus Páll-Gergely 2013

The following species-group taxa are described as new to science:

Genus2 species3 u. sp.

Chersaecia species1 u. sp.

Chersaecia shiroiensis subspecies1 u. ssp.

Endothyrella species4 u. sp.

Endothyrella species5 u. sp.

Endothyrella species6, u. sp.

Endothyrella species7 u. sp.

Endothyrella species8 u. sp.

Gudeodiscus (Gudeodiscus) concavus Páll-Gergely 2013

Gudeodiscus (Gudeodiscus) giardi szekeresi Páll-Gergely & Hunyadi 2013

Gudeodiscus (Gudeodiscus) giardi oharai Páll-Gergely 2013

Gudeodiscus (Gudeodiscus) hemmeni Páll-Gergely & Hunyadi Páll-Gergely 2015
Gudeodiscus (Gudeodiscus) marmoreus Páll-Gergely 2014
Gudeodiscus (Gudeodiscus) messengeri raheemi Páll-Gergely & Hunyadi Páll-Gergely 2015
Gudeodiscus (Gudeodiscus) soosi Páll-Gergely 2013
Gudeodiscus (Gudeodiscus) ursula Páll-Gergely & Hunyadi 2013
Gudeodiscus (Gudeodiscus) yanghaoi Páll-Gergely & Hunyadi 2013
Gudeodiscus (Gudeodiscus) yunnanensis Páll-Gergely 2013
Gudeodiscus (Veludiscus) emigrans otanii Páll-Gergely & Hunyadi 2013
Gudeodiscus (Veludiscus) eroessi Páll-Gergely & Hunyadi 2013
Gudeodiscus (Veludiscus) eroessi fuscus Páll-Gergely & Hunyadi 2013
Gudeodiscus (Veludiscus) eroessi hemisculptus Páll-Gergely 2013
Gudeodiscus (Veludiscus) goliath Páll-Gergely & Hunyadi 2013
Gudeodiscus (Veludiscus) okuboi Páll-Gergely & Hunyadi 2013
Gudeodiscus (Veludiscus) pulvinaris robustus Páll-Gergely & Hunyadi 2013
Plectopylis species2 u. sp.
Sicradiscus feheri Páll-Gergely & Hunyadi 2013
Sicradiscus transitus Páll-Gergely 2013
Sinicola asamiana Páll-Gergely 2013
Sinicola schmackeri Páll-Gergely 2013
Sinicola stenomphala Páll-Gergely & Hunyadi 2013
Sinicola vargabalinti Páll-Gergely 2014

*Endothyrella nomenovum*1 Páll-Gergely nomen novum is proposed to replace *Helix (Plectopylis) minor* Godwin-Austen 1879, which is a junior homonym of *Helix nemoralis* var. *minor* Charpentier, 1837.

New synonyms

The differences between the following taxa and other species can be interpreted as intraspecific differences.

Therefore they are handled as new synonyms:

brachydiscus Godwin-Austen 1879, *leucochila* Gude 1897, *lissochlamys* Gude 1897, *magna* Gude 1897, *ponsonbyi* Godwin-Austen 1888, *leiophis* Benson 1860, *pseudophis* Godwin-Austen 1875, *degerbolae* Solem 1966; *nagaensis* Godwin-Austen 1875, *kengtungensis* Gude 1914, *repercussa* Gould 1856, *municipurensis* Godwin-Austen 1875, *persimilis* Gude 1901, *tenuis* Gude 1901, *bavayi* Gude 1901, *lepidus* Gude 1900, *congesta* Gude 1898, *soror* Gude 1908, *moellendorffi* Gude 1901, *fallax* Gude 1909, *gouldingi* Gude 1909, *anterides* Gude 1909, *verecundus* Gude 1909, *wernereri* Páll-Gergely 2013, *continentalis* Möllendorff 1885, *hirsutus* Möllendorff 1901, *jovia* Mabilbe 1887, *pilsbryana* Gude 1901.

Revision of Gude's (1899e) generic division

All of Gude's (1899e) genera had to be redefined and several species had to be moved to other existing or new genera. The generic status of known species had to be changed in 52 % of the cases (38 out of 73).

Genus *Endoplon* sensu Gude (1899e and 1915): Gude (1899d) chose *Helix brachyplecta* Benson 1863 for the type species of *Endoplon* and placed a similar and nearby occurring species (*Plectopylis smithiana* Gude 1897) also in this genus. These taxa together with the Vietnamese species corresponded to one section in Gude's (1899e) system, which is based on two selected shell characters (direction of coiling and structure of palatal plicae). *E. brachyplecta* and *E. smithiana* however, were described from Attaram, Burma, which lies geographically very distant (at least 800 km) from the area of all other known *Endoplon* species (Southern China and Northern Vietnam). For the Chinese and Vietnamese former *Endoplon* species, a new genus, *Gudeodiscus* Páll-Gergely 2013 is erected. *Endoplon* and *Gudeodiscus* differ in the following shell characters: (1) The apertural fold is always short or missing in *Gudeodiscus*, while in *Endoplon*, it reaches up to one quarter of the last whorl. (2) The protoconch in all *Gudeodiscus* is very finely, regularly ribbed, while that of *Endoplon* is smooth with irregular growth lines. This protoconch structure of *Endoplon* resembles that of *Plectopylis* s. s. species. (3) The concave side of the posterior lamella of *E. brachyplecta* is facing towards the aperture, while in all species of *Gudeodiscus*, the convex side is directed anteriorly. (4) *E. smithiana* has two converging denticles on the parietal wall, while in *Gudeodiscus*, the plicae in the same position are usually parallel with the sutures. (5) The middle palatal plicae (third-fifth) of *Gudeodiscus* have usually a depressed Z-shape. In *Endoplon* they are short and slightly curved, almost parallel with

each other. Superficially, the robust shells of *E. smithiana* and *E. brachyplecta* resemble those of *Plectopylis* s. s. species, which are nevertheless all sinistral. *Plectopylis* (*Endoplion*) *aborensis* was placed into the subgenus *Endoplion* on the basis of simple, oblique palatal plicae. All other shell characters and geographical distribution suggest that *P. aborensis* belongs to *Endothyrella*.

Genus *Chersaecia* sensu Gude (1899e and 1915): This genus was apparently used as a "dust bin" of Western Plectopylidae, because the species which were included in this genus Gude (1899e) are now classified into five genera (including *Chersaecia*). Members of the genus Genus1 are conchologically similar to *Chersaecia* and differ only in the anatomy, which was unknown to Gude. The other three genera recognized by me (Genus2, *Endothyrella*, Genus3), on the other hand, are mainly defined on conchological basis. The most important differences between *Chersaecia* and those three genera are the tuberculated protoconch in *Chersaecia* and the ribbed protoconch in Genus2, *Endothyrella* and Genus3, and the presence (*Chersaecia*) and absence (Genus2, *Endothyrella*, Genus3) of an apertural fold.

Genus *Endothyrella* sensu Gude (1899e and 1915): All species formerly assigned to *Endothyrella* (Gude 1899e, 1915) were correctly placed in that genus. However, some *Chersaecia* sensu Gude (1899c, 1915) species belong to *Endothyrella*. Three sinistral (*bedfordi*, *brahma*, *williamsoni*) and two dextral (*oglei*, *serica*) species are moved from *Chersaecia* to *Endothyrella* based on the ribbed protoconch and the absence of the apertural fold. Another species which was assigned to *Chersaecia* (*Plectopylis munipurensis*) is the synonym of *Endothyrella serica*.

Genus *Sinicola* sensu Gude (1899e and 1915): Gude defined the genus *Sinicola* on the basis of the horizontal palatal plicae only. This resulted in the placement of species to *Sinicola* which are only distantly related to *Sinicola* species. *Plectopylis babbagei* was placed in *Sinicola* by Gude (1915), but the periostracal folds standing in three rows on the body whorl and geographical area suggests that *P. babbagei* is the member of *Endothyrella*. *Plectopylis emigrans*, *P. multispira*, *P. pulvinaris*, *P. fruhstorferi* and *P. infralevis* were all assigned to *Sinicola*. All of them, however, belong to other genera (*Gudeodiscus*, *Halongella*) based on the rounded body whorl (keeled in *Sinicola*) and anatomical information.

Some former *Sinicola* species which possess two lamellae (or only the anterior lamella) instead of only the posterior one were moved to a new genus, *Sicradiscus*.

Genus *Plectopylis* sensu Gude (1899e): Gude (1899e) defined *Plectopylis* on the basis of the morphology of the palatal plicae. Namely, one vertical plate with three horizontal folds above, and one below. The arrangement, however, also occurs in some *Chersaecia* (sensu Gude 1899e) species. Although not mentioned in the diagnoses, the peculiarity of Gude's subdivision is that all of his *Plectopylis* species possess two lamellae, whereas all *Chersaecia* only one. My investigations showed that there are transitional character states between the two and one lamella types (see under Chapter 8). Therefore, this cannot be a distinguishing character between two genera. In my system I retained only those species in *Plectopylis* which had the upper end of the lamellae fused. All other, former *Plectopylis* species have been moved to *Chersaecia*.

Chapter 9d: Discussion: Anatomy and biology

Out of approximately 120 plectopylid species, genital anatomy is only known in roughly 35 taxa. Some were described before my revision: *Plectopylis bensoni* (under the name *achatina*) and *P. cyclaspis* (both in Stoliczka 1871); *Chersaecia perarcta simplex* (in the original description: Solem 1966); *Endothyrella pinacis* (Godwin-Austen 1889–1914, Schileyko 1999); *Sicradiscus hirasei* (Azuma & Azuma 1984), *Sic. ishizakii*, (Chang & Ookubo 1999). Stoliczka (1871) mentioned that he also "examined the animal" of *Plectopylis macromphalus* (W. Blanford 1870) (now genus *Endothyrella*), but described only the anatomy of *Plectopylis achatina* and *P. cyclaspis*. The anatomy of the following species were examined by me: Genus1 *dextrorsa*, *Plectopylis bensoni*, *Plectopylis* species2 u. sp., *Chersaecia perrierae*, *Ch. shanensis*, *E. blanda*, *E. plectostoma*, *E. fultoni*, *Halongella schlumbergeri*, *H. fruhstorferi*, Genus3 *laomontana*, *Sic. mansuyi*, *Sic. schistoptychia*, *Sic. transitus*, *Sic. inivius*, *Sinicola fimbriosa*, *Sin. emoriens*, *Sin. asamiana*, *Sin. murata*, *Sin. reserata azona*, *Sin. stenochila*, *Gudeodiscus pulvinaris robustus*, *G. multispira*, *G. phlyariis*, *G. emoriens otanii*, *G. eroessi eroessi*, *G. giardi giardi*, *G. okuboi*, *G. pulvinaris pulvinaris*, *G. villedaryi*, *G. fischeri*, *G. messengeri raheemi*.

The genital organs of Plectopylidae are rather simple. Most species share the simple penis and epiphallus with or without penial caecum, having the retractor muscle (if present) attached to the penis-epiphallus transition or on the

penial caecum. Vas deferens joins epiphallus apically without flagellum, and the distal end of the vas deferens is usually thickened and curvy. The female genitalia is also simple, with usually (1) a "vaginal bulb", which is a thickening at the middle of the vagina where the organ is folded ("turns back") in the animal when it is withdrawn into the shell, (2) muscle fibres which fix the vagina to the diaphragm, and (3) a long bursa copulatrix and a diverticulum of various length.

The epiphallus is absent in some taxa (*Chersaecia perarcta simplex*, *Ch. perrieriae*, Genus3 *laomontana*). In those taxa the vas deferens originates from the wall of the penis (*Chersaecia* spp.) and the vagina (Genus3 *laomontana*). The penial caecum and the diverticulum are absent in some taxa. However, it is relatively difficult to obtain reliable information. The diverticulum is very slender and it is attached to the membrane of the uterus, and therefore, impossible to dissect out occasionally. The penial caecum is a blindly ended organ at the meeting point of the penis and the epiphallus. The penis-epiphallus tube is folded at their joining point, and the two organs are attached to each other usually by weak membrane. This physical arrangement sometimes makes it difficult to decide that penial caecum is present or not. For example, in case of *Sinicola stenochila* and *Gudeodiscus eroessi* there is a well-developed caecum, whereas it is clearly absent in both *Halongella* species. In other species, such as *Chersaecia shanensis* it is difficult to be objective about the presence or absence of the caecum. *Gudeodiscus*, *Sinicola* and *Sicradiscus* species often have a well distinguished caecum, but *Plectopylis*, *Chersaecia* and *Halongella* species usually lack it.

Diverticulum

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". I found a spermatophore inside this organ of *G. 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. Only exception known before this study was the subfamily Garniierinae (family Clausiliidae), in which the diverticulum derives from the pedunculus (Szekeres 1998).

Inner wall of the male organs

The inner walls of the male genital organs, especially the penis, show a huge diversity across the genera *Gudeodiscus*, *Halongella*, *Sicradiscus* and *Sinicola*. *Sinicola* and *Halongella* 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. messengeri raheemi* u. ssp.) on the opened penial wall. *Sicradiscus* species have both types of penial sculpture. 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 & 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 was difficult to remove. The SEM images of removed claws revealed that the handle-like part 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* 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 fixed to the internal wall, because to my knowledge, hook-less specimens have not been reported in contrast to those in Plectopylidae. Those of *Cryptazeca* and Streptaxidae are not calcareous (Gómez 1991, Visser 1973, Verdcourt 1979, 1985), 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. I found that 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. My 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* 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 *Simicola* 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 messengeri raheemi* has deep sinuses with the calcareous granules. *Gudeodiscus giardi giardi* has pockets formed by two neighbouring papillae (Páll-Gergely & 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. messengeri 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*.

I used specimens that were fixed in 70% ethanol for this investigation. Thus, at this stage of study, I was not able to rule out a possibility some of them 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 2.1–2.4). 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. My 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 non-calcareous hooks in other groups. It has been classically postulated that these may function for mechanical stimulation for mating success similarly to love darts and other penial structure (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 *Sinistrexica*. 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. The present study provides a systematic ground for further studies on the evolution of mating apparatus inside the penis.

Radula

The only information on plectopylid radula was published by Stoliczka (1871) (*Plectopylis achatina*, *P. cyclaspis* and *Endothyrella pinacis*), Solem (1966) (*Chersaecia perarctica simplex*) Chang and Ookubo (1999) (*Sicradiscus ishizakii*). My 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 *Endothyrella*, *Sicradiscus*, *Simicola* 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*, *Chersaecia*, Genus1, and *Gudeodiscus* (*Veludiscus*) 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 shallow incision between the inner two cusps. Stoliczka (1871) mentioned that *Endothyrella pinacis* (that time *Plectopylis pinacis*) has larger central tooth than the two *Plectopylis* species, but he have not provided description or drawing of the marginal teeth.

Chapter 9e: Biogeography and habitat

Possible origin of the family Plectopylidae

The genera of Tribe1 are distributed from northeastern India to Northern Malaysia, inhabiting large part of Myanmar and Northern Thailand. The genera of Tribe2 inhabit Eastern Asia from Nepal to Okinawa, throughout Northern Myanmar, Northern Thailand, Northern Laos, Northern Vietnam, and several Southern Chinese Provinces (Figure 7.130). Since the subfamily Subfamily1 is known from eastern Myanmar, the geographic origin of the family is probably in western Indochina. Thus, the family seem to have a Laurasian origin. The radiation of the family in Eastern direction happened earlier than the Middle Eocene, because the genus *Plectopyloides* which is known from that time, is known from China, near Beijing. The centre of the diversity of the "Eastern Plectopylidae" is Northern Vietnam and Southern China, especially Guangxi Province. North and East from that region the number of species and genera is decreasing.

Geographical coverage of the Vietnamese plectopylid fauna

The most well-known area in terms of the family Plectopylidae is Northern Vietnam. 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 7.109). I was able to examine only a few newly collected northern Tonkinese samples. Therefore, my knowledge on those species reported from the northern border region of Vietnam is mainly based on museum specimens. On the other hand, I 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. I was able to examine plectopylid specimens from western Tonkin 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 lowlands of the Red River, although these areas may not probably provide suitable habitats for land snails that prefer limestone outcrops or mountainous areas. Molluscan fauna in the border region of Son La and Yên Bái Provinces (Phan Xi Păng= "Farsipan" Mountain and its vicinity) is nearly unknown, maybe due to their low 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 Nghe 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.

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.

Chapter 9f: Relevance of my study

During the systematic revision of the family Plectopylidae I examined all available specimens in public institutions and private collections. I examined several morphological characters and identified the ones which are useful to diagnose taxa. I revised all previously described species, subspecies and varieties. I described taxa new to science. I revised the previously proposed subdivision of the family critically and proposed a new system based on morphological information. The systematic revision revealed some major questions regarding the systematic positions of plectopylid taxa. These are:

- (1) Is Corillidae really the sister family of the Plectopylidae?
- (2) Is Genus1 really the most basal lineage of the Plectopylidae?
- (3) What is the systematic status of *Sicradiscus* species in relation to the genera *Gudeodiscus* and *Simicola*?
- (4) Which is the closest relative of the genus *Endothyrella*?
- (5) The systematic position of the genera *Endoplon* and Genus2, and the dextral members of *Endothyrella* are questionable due to the unknown anatomy.

My system provides a taxonomic basis for studying the evolution of left-right asymmetry in the Plectopylidae and the evolution of the mating behaviour using "male weapons", which probably play a role in the sexual conflict.

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Chapter 11: References

- Adams, H. & Adams, A. (1855): The genera of recent Mollusca; arranged according to their organization. In three volumes.-Vol. II. - pp. [1-3], 1-661. London. (Van Voorst).
- Albers, J.C. (1850): Die Heliceen nach natürlicher Verwandtschaft systematisch geordnet. Berlin, Th. Chr. Fr. Enslin, 262 pp.
- Allmon W.D. 1992. Genera in paleontology: Definition and significance. *Historical Biology*, 6(2): 149-158.
- Ancey, C-F. (1882): Coquilles de Chine Centrale Nouvelles ou peu Connues. *Le Naturaliste: Journal des échanges et des nouvelles*, 4: 44-45.
- Ancey, C-F. (1885): Nouvelles Contributions Malacologiques. Sur divers Mollusques de l'Empire Chinois. *Bulletins de la Société Malacologique de France*, 2: 113-137.
- Ancey, C.-F. (1887). Description of new genera or subgenera of Helicidae. *Conchologists Exchange*. 1: 53-54, 64, 75-76; 2: 22-23, 38-39.
- Ancey, C.-F. (1888): Mollusques du Haut-Tonkin (Récoltes de M. Villedary). *Le Naturaliste: journal des échanges et des nouvelles*, 2 (10): 70-72.
- Asami, T., Cowie R.H. & Ohbayashi K. (1998): Evolution of mirror images by sexually asymmetric mating behavior in hermaphroditic snails. *American Naturalist*, 152: 225-236. doi:10.1086/286163.
- Atkinson, J.W. & Atkinson, K.E.H. (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.
- Azuma, M. & Azuma, Y. (1984): Distribution of land snails of Miyako islands, the South-western Okinawa, Japan (1st report). *Satuki*, 20: 85-98.
- Bachmann, O. & Gredler, V. (1894): Zur Conchylienfauna von China. XVIII. Stück. *Annalen des Kaiserlich-Königlichen Naturhistorischen Hofmuseums*, 9 (3): 415-429.
- Baker, H.B. (1925): Agnathomorphous Aulacopoda. *The Nautilus* 38 (3): 86-89.
- Baker, H.B. (1963): Type land snails in the Academy of Natural Sciences of Philadelphia, Part II. Land Pulmonata, exclusive of North America north of Mexico. *Proceedings of the Academy of Natural Sciences of Philadelphia* 115 (8): 191-259.
- Balvanera, P., Pfisterer, A.B, Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. & Schmid, B (2006): Quantifying the evidence for biodiversity effects on ecosystem functioning and services: 1146-1156.
- Bartha F. & Soós L. (1955): Die pliozäne Molluskenfauna von Balatonszentgyörgy. *Annales historico-naturales Musei Nationalis Hungarici*, 6: 51-72.
- Bastian, F. Parmentier, G., Roux, J., Moretti, S., Laudet, V. & Robinson-Rechavi, M. (2008): Bgee: integrating and comparing heterogeneous transcriptome data among species. In *Data Integration in the Life Sciences*. Springer, New York, pp. 124-131.
- Bebber, D.P., Wood, J.R.I., Barker, C. & Scotland, R.W. (2014): Author inflation masks global capacity for species discovery in flowering plants. *New Phytologist* 201: 700-706.
- Benitez, H.A. (2014): Is the Fever for High Impact a Disadvantage for Systematists? *Neotropical Entomology*, DOI 10.1007/s13744-014-0217-x
- Benson, W.H. (1836): Descriptive Catalogue of Terrestrial and Fluvial Testacea, chiefly from the North-East Frontier of Bengal. *Journal of the Asiatic Society of Bengal* 5: 350-358.
- Benson, W.H. (1859a): Descriptions of new species of *Helix*, *Streptaxis*, and *Vitrina*, collected by Mr. W. Theobald, jun. in Burmah, the Khasia Hills, and Hindustan. *Annals and Magazine of Natural History*, 3 (3): 184-188.
- Benson, W.H. (1859b): Descriptions of new Helicidae contained in the Darjiling collections of Messrs. W. T and H. F. Blanford. *Annals and Magazine of Natural History*, 3 (3): 265-273.
- Benson, W.H. (1859c): [There being already a *Helix catinus*...] (Note). *Annals and Magazine of Natural History*, 3 (3): 273.
- Benson, W.H. (1859d): Notes on the Animals of *Rhaphaulus chrysalis*, *Pupina artata*, *Otopopa clausum*, *Helix achatina*, and *H. pylaïca*. *Annals and Magazine of Natural History*, 3 (4): 93-96.

- Benson, W.H. (1860a): Notes on *Plectopylis*, a group a Helicidae distinguished by several internal plicate ephiphragms; with the characters of a new species. *Annals and Magazine of Natural History*, 3 (5): 243–247.
- Benson, W.H. (1860b): Notes on the Subgenus *Corilla*, H. & A. Adams; and on the Group Plectopylis, BENSON; also on *Pollicaria*, Gould, and *Hybocystis*, Benson. *Annals and Magazine of Natural History*, 3 (6): 98–100.
- Benson, W.H. (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.
- Bentham-Jutting, van, W.S.S. (1960): Some notes on land and freshwater Mollusca of Malaya. *Basteria*, 24, 10–20.
- Berry, A.J. (1963): An introduction to the non-marine molluscs of Malaya. *Malayan Nature Journal*, 17, 1–17.
- Blackwelder, R.E. (1967): *Taxonomy: a text and reference book*. Wiley, New York.
- Blanford, W.T. (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.
- Blanford, W.T. (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.
- Blanford, W.T. (1870): Contributions to Indian Malacology No. 9. Description of new species of Paludomus, Cremnoconchus, Cyclostoma and of Helicidae from various parts of India. *Journal of the Asiatic Society of Bengal*, 39 (2): 9–25.
- Bouchet, P. (2006). The Magnitude of Marine Biodiversity. Chapter 2 in Duarte, C.M. (ed.). *The Exploration of Marine Biodiversity: scientific and technological challenges*. Bilbao: Fundación BBVA. Available online at <http://www.marinebarcoding.org/userfiles/File/bouchetmagnitude.pdf>
- Bouchet, P. & Rocroi, J.-P. (2005): Classification and Nomenclator of Gastropod Families. *Malacologia*, 47 (1–2): 1–397.
- Bouchet P. & Rocroi J.-P. (Ed.); Frýda J., Hausdorf B., Ponder W., Valdes A. & Warén A. (2005): Classification and nomenclator of gastropod families. *Malacologia: International Journal of Malacology*, 47(1-2). ConchBooks: Hackenheim, Germany. ISBN 3-925919-72-4. 397 pp.
- Brandt, A.J. (1977): An annotated checklist of the non-marine molluscs of Hong Kong. In: Morton, B. (ed.): *The malacofauna of Hong Kong and Southern China*, 1–345. Hong Kong (Hong Kong University Press).
- Burbrink, F.T., Lawson, R. & Slowinski, J.B. (2000): Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*), a critique of the subspecies concept. *Evolution* 54: 2107–2118.
- de Carvalho, M.R., Bockmann, F.A., Amorim, D.S., de Vivo, M., de Toldeo-Piza, M., Menezes, N.A., de Figueiredo, J.L., Castro, R.M.C., Gill, A.C., McEachran, J.D., Compagno, L.J.V., Schelly, R.C., Britz, R., Lundberg, J.G., Vari, R.P. & Nelson, G. (2005): Revisiting the taxonomic impediment. *Science* 307: 353.
- de Carvalho, M.R., Bockmann, F.A., Amorim, D.S., Brandão, C.R.F., de Vivo, M., de Figueiredo, J.L., Britski, H.A., de Pinna, M.C.C., Menezes, N.A., Marques, F.P.L., Papavero, N., Canello, E.M., Crisci, J.V., McEachran, J.D., Schelly, R.C., Lundberg, J.G., Gill, A.C., Britz, R., Wheeler, Q.D., Stiassny, M.L.J., Parenti, L.R., Page, L.M., Wheeler, W.C., Faivovich, J., Vari, R.P., Grande, L., Humphries, C.J., DeSalle, R., Ebach, M.C. & Nelson, G. (2007): Taxonomic impediment or impediment to taxonomy? A commentary on systematics and the cybertaxonomic-automation paradigm. *BMC Evolutionary Biology* 34: 140–143.
- de Carvalho, M.R., Ebach, M.C. (2010): Death of the specialist, rise of the machinist. *Hist. Phil. Life Sci.* 31, 461–464.
- de Carvalho M.R., Ebach M.C., Williams D.M., Nihei S.S., Rodrigues M.T., Grant T., Silveira L.F., Gill A.C., Schelly R.C., Sparks J.S., Bockmann F.A., Séret B., Ho H.-C., Grande L., Rieppel O., Dubois A., Ohler A., Faivovich J., Assis L.C.S., Wheeler Q.D., Goldstein P.Z., Almeida E.A.B. de, Valdecassas A.G. & Nelson G.J. (2014): Does counting species count as taxonomy? On misrepresenting systematics, yet again. *Cladistics* 30: 322–329.
- Chang, K.M. & Ookubo, K. (1999): Anatomy and Systematics on *Plectopylis (Sinicola) ishizakii* Kuroda, 1941 from Taiwan. *Bulletin of Malacology, Taiwan ROC*, 23: 21–28.
- Charpentier, J. de (1837): *Catalogue des mollusques terrestres et fluviatiles de la Suisse. Formant la seconde partie de la faune Helvétique*. Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften - Nouveaux Mémoires de la Société Helvétique des Sciences Naturelles 1 (2): 1–28, Tab. I–II.

- Chapman, A.D. (2009): Numbers of Living Species in Australia and the World, 2nd edition. Australian Biological Resources Study, Canberra. Accessed 12 January 2010. ISBN 978-0-642-56860-1 (printed); ISBN 978-0-642-56861-8 (online).
- Chase, R. & Blanchard, K.C. (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.
- Chen, N. & Gao, X. (1988): 浙江省陆生贝类调查及区系分析 (Survey of the land snail fauna of Zhajiang). *Sichuan Journal of Zoology* 7 (3): 31–33. (In Chinese)
- Costello, M.J., Wilson, S. & Houlding, B. (2012): Predicting Total Global Species Richness Using Rates of Species Description and Estimates of Taxonomic Effort. *Systematic Biology* 61 (5): 871–883.
- Costello, M.J., Wilson, S. & Houlding, B. (2013a): More Taxonomists Describing Significantly Fewer Species per Unit Effort May Indicate That Most Species Have Been Discovered *Systematic Biology* 62 (4): 616–624.
- Costello, M.J., May, R.M. & Stork, N. E. (2013b): Can we name earth's species before they go extinct? *Science* 339, 413–416.
- Coyne, J. A., & Orr, HA. (2004): *Speciation*. Sinauer, Sunderland, MA.
- Cuezzo, M.G. & Miranda, M.J. (2009): Systematic position and anatomy of *Drepanostomella tucma* Hylton Scott, 1948 (Stylommatophora: Scolodontidae). *Journal of Conchology* 39 (6): 683–691.
- Dance, S.P. (1986): *A History of shell collecting*. E. J. Brill, Leiden, 265 pp.
- Dautzenberg, Ph. & d'Hamonville, B.L. (1887): Description d'Espèces nouvelles du Tonkin sur quelques autres Mollusques de la même région. *Journal de Conchyliologie*, 35: 213–225.
- Dautzenberg, Ph. & 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.
- Dautzenberg, Ph. & 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 (4): 343–371.
- Dautzenberg, Ph. & Fischer, H. (1908): Liste des mollusques récoltés par M. MANSUY en Indo-Chine et description d'espèces nouvelles. *Journal de Conchyliologie*, 56: 169–217.
- de Queiroz, K. (1998): The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. Pp. 57–75 in D. J. Howard and S. H. Berlocher, eds. *Endless forms: species and speciation*. Oxford Univ. Press, New York, Oxford.
- de Queiroz, K. (2005a): Ernst Mayr and the modern concept of species. *Proc. Natl. Acad. Sci. USA* 102:6600–6607.
- de Queiroz, K. (2005b): Different species problems and their resolution. *BioEssays* 27:1263–1269.
- Degner, E. (1923): Zur Anatomie und systematischen Stellung von *Sculptaria* Pfeiffer. *Archiv für Molluskenkunde* 55(4): 14–160. Plate 6, page 157.
- Deschka, G. & Dimic, N. (1986): *Cameraria ohridella* n. sp. aus Mazedonien, Jugoslawien (Lepidoptera, Lithocolletidae). *Acta entomologica Jugoslavica* 22: 11–23.
- Deshayes, G.-P. (1870): Diagnoses d'Espèces Nouvelles de Mollusques Terrestres et Fluviales de la Principauté de Moupin, Thibet Oriental. *Nouvelles archives du Muséum d'Histoire Naturelle*, 6: 19–27.
- Deshayes, G.-P. (1873): Description de Quelques Espèces de Mollusques Nouveaux ou peu connus Envoyés de la Chine par M. l'Abbé A. David. *Nouvelles archives du Muséum d'Histoire Naturelle*, 9: 3–14.
- Dirzo, R., Raven, P.H. (2003): Global state of biodiversity and loss. *Annu Rev Environ Resour* 28:137–167
- Döring, A. (1875): Apuntes sobre la Fauna de Moluscos de la República Argentina (segunda parte). *Boletín de la Academia Nacional de Ciencias Exactas Univ. Córdoba* 1: 432–460.
- Ebach, M.C., Valdecasas, A.G. & Wheeler, Q.D. (2011): Impediments to taxonomy and users of taxonomy: accessibility and impact evaluation. *Cladistics* 27:1–8.
- Edwards, F.W. (1953): Genera and subgenera. *Systematic Zoology*, 2(3): 135.
- Ehrmann, P. (1922): Land- und Süßwasserschnecken aus den südl. Schan-Staaten, Hinterindien. *Sitzungsberichte der naturforschender Gesellschaft zu Leipzig*, 45–48, 1–28.
- Eldredge, N., & Cracraft, J. (1980): *Phylogenetic patterns and the evolutionary process*. Columbia Univ. Press, New York.
- Erwin, D., Valentine, J.W. & Jablonski, D. (1997): The origin of animal body plans. *American Scientist* 85: 126–137.

- Evenhuis, N.L. (2007): Helping solve the “other” taxonomic impediment: completing the Eight Steps to Total Enlightenment and Taxonomic Nirvana. *Zootaxa*, 1407, 3–12.
- Fischer, H. (1898a): Notes sur la Faune du Haut-Tonkin III. Liste des Mollusques Recueillis par le Dr. A. Billet. *Bulletin Biologique de la France et de la Belgique*, 28: 310–338.
- Fischer, H. (1898b): Description d’une espèce nouvelle de *Plectopylis*. *Journal de Conchyliologie*, 46 (3): 214–218.
- Fischer, H. (1899a): Notes sur la Faune du Haut-Tonkin V. Description d’une Espèce Nouvelle de *Plectopylis*. *Bulletin Biologique de la France et de la Belgique*, 5 (32): 329–332.
- Fischer, H. (1899b): Description d’une espèce nouvelle de *Plectopylis*. *Journal de Conchyliologie*, 46 (3): 214–218.
- Fischer, H. & Dautzenberg, Ph. (1904): Catalogue des mollusques terrestres et fluviatiles de l’Indo-Chine orientale cites jusqu’à ce jour. *Mission Pavie, Études diverses*, 3: 390–442.
- Fitzpatrick, J.W. (2010): Subspecies are for convenience. *Ornith Mon* 67: 54–61
- Fontaine, B., van Achterberg, K., Alonso-Zarazaga, M.A., Araujo, R., Asche, M., Aspöck, H., Aspöck, U., Audisio, P., Aukema, B., Bailly, N., Balsamo, M., Bank, R.A., Belfiore, C., Bogdanowicz, W., Boxshall, G., Burckhardt, D., Chylarecki, P., Deharveng, L., Dubois, A., Enghoff, H., Fochetti, R., Fontaine, C., Gargominy, O., Lopez, M.S., Goujet, D., Harvey, M., Heller, K.G., van Helsdingen, P., Hoch, H., De Jong, Y., Karsholt, O., Los, W., Magowski, W., Massard, J.A., McInnes, S.J., Mendes, L.F., Mey, E., Michelsen, V., Minelli, A., Nafria, J.M., van Nieukerken, E.J., Pape, T., De Prins, W., Ramos, M., Ricci, C., Roselaar, C., Rota, E., Segers, H., Timm, T., van Tol, J. & Bouchet, P. (2012): New species in the old world: Europe as a frontier in biodiversity exploration, a test bed for 21st century taxonomy. *PLoS ONE*. 2012, 7(5):e36881
- Franz, N.M (2005): On the lack of good scientific reasons for the growing phylogeny/classification gap. *Cladistics* 21: 495–500.
- Frost, D.R. & Hillis, D.M. (1990): Species concepts and practice: herpetological applications. *Herpetologica* 46: 87–104.
- Fulton, H. (1914): On *Stenopylis*, a proposed new genus of Endodontidae. *Annals and Magazine of Natural History* 8 (14): 163–164.
- Gittenberger, E. (2000): Alternative pathways in the development of the clausilial apparatus in shells of *Albinaria* and *Isabellaria* (Gastropoda: Pulmonata: Clausiliidae). – *Basteria*, 64 (1–3): 29–32.
- Gmelin, J.F. (1791): *Caroli a Linné, systema naturae*. Tom. I. Pars VI.: 3021–3910. Lipsiae. (Beer).
- Godfray, H.C.J. (2007): Linnaeus in the information age. *Nature* 446, 259–260.
- Godwin-Austen, H.H. (1875a): Supplementary Notes on the Species of *Helicidae* of the subgenus *Plectopylis*. *Proceedings of the Zoological Society of London*, 43–44.
- Godwin-Austen, H.H. (1875b): 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.
- Godwin-Austen, H.H. (1879a): On new species of the Genus *Plectopylis* of the Family *Helicidae*. *Journal of the Asiatic Society of Bengal*, 48 (2): 1–4, plate 1.
- Godwin-Austen, H.H. (1879b): Description of two new Species of *Plectopylis*, a Subgenus of *Helicidae*. *The Annals and Magazine of Natural History*, 5 (4): 163–164.
- Godwin-Austen, H.H. (1888): On some Land-Mollusks from Burmah, with Descriptions of some new Species. *Proceedings of the Zoological Society of London*, 240–245.
- Godwin-Austen, H.H. (1889–1914): Land and freshwater Mollusca of India, including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burma, Pegu, Tenasserim, Malaya Peninsula, Ceylon and other islands of the Indian Ocean; Supplementary to Masers Theobald and Hanley's *Conchologia Indica*. Vol II. 1–442; London (Taylor and Francis).
- Godwin-Austen, H.H. (1892): Description of a new Species of *Helix* of the subgenus *Plectopylis*. *The Annals and Magazine of Natural History*, 6 (10): 300–301.
- Godwin-Austen, H.H. (1895): Notes on, and drawings of, the animals of various Indian Land Mollusca (Pulmonifera). *Journal of the Asiatic Society of Bengal*, 64 (2): 151–156. Plate 7.
- Gómez, B.J. (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.

- Gould, A.A. (1846): [Dr. Gould exhibited a collection of shells, sent from Tavoy, in Burmah, by the Rev. Mr. Mason. Among them he distinguished and characterized the following undescribed species]. *Proceedings of the Boston Society of Natural History*, 2, 98–100.
- Gould, A.A. (1847): [Dr. Gould described new shells...]. *Proceedings of the Boston Society of Natural History*, 2, 218–221.
- Gould, A.A. (1856): [Dr. A. A. Gould presented the following descriptions of shells]. *Proceedings of the Boston Society of Natural History*, 6, 11–16.
- Gould, A.A. (1859): [Descriptions of Shells Collected at the North Pacific Exploring Expedition]. *Proceedings of the Boston Society of Natural History*, 6: 422–426.
- Gould, A.A. (1862): *Otia Conchologica: Descriptions of shells and molluscs from 1839 to 1862*. Boston. Gould and Lincoln, 59 Washington Street. 256 pp.
- Govindan, A., Yadagiri, K., Ravindran, C.N. & Kalyanasundar, R. (1998): A field guide on Cretaceous sequences of Tiruchirapalli Area, Cauvery Basin, India; Oil and Natural Gas Corporation Limited, 53 p.
- Gredler, V. (1881): Zur Conchylien-Fauna von China. II. Stück. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 8: 10–33.
- Gredler, V. (1887a): Zur Conchylien-Fauna von China. XIII. Stück. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 14: 343–373.
- Gredler, V. (1887b): Zur Conchylien-Fauna von China. X. Stück. *Uebersicht der continentalen chinesischen Binnenschnecken. Malakozoologische Blätter*, 9: 120–163.
- Gredler, V. (1889a): Zur Conchylien-Fauna von China. XIV. Stück. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 21: 155–163.
- Gredler, V. (1889b): Kritische Fragmente. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 21: 195–206.
- Grego, J., Van Luong, H. Van Pham, S. & Miklós Szekeres (2014): Vietnamese Clausiliidae (Gastropoda: Pulmonata): New taxa and novel distribution data. *Journal of Conchology* 41 (6): 749–757.
- Groenenberg, D.S.J., Neubert, E. & Gittenberger, E (2011): Reappraisal of the “Molecular phylogeny of Western Palearctic Helicidae s.l. (Gastropoda: Stylommatophora)”: When poor science meets GenBank. *Molecular Phylogenetics and Evolution* 61: 914–923
- Gude, G.K. (1896a): Armature of Helicoid landshells. And a New Species of *Corilla*. *Science Gossip*, 3: 88–92.
- Gude, G.K. (1896b): Armature of Helicoid landshells. *Science Gossip*, 3: 126–128.
- Gude, G.K. (1896c): Armature of Helicoid landshells. *Science Gossip*, 3: 154–156.
- Gude, G.K. (1896d): Armature of Helicoid landshells. *Science Gossip*, 3: 178–181.
- Gude, G.K. (1897a): Armature of Helicoid landshells. *Science Gossip*, 3: 204–207.
- Gude, G.K. (1897b): Armature of Helicoid landshells. *Science Gossip*, 3: 244–246.
- Gude, G.K. (1897c): Armature of Helicoid landshells and new forms of *Plectopylis*. *Science Gossip*, 3: 274–276.
- Gude, G.K. (1897d): Armature of Helicoid landshells and new forms of *Plectopylis*. *Science Gossip*, 3: 300–301.
- Gude, G.K. (1897e): Armature of Helicoid landshells and new forms of *Plectopylis*. *Science Gossip*, 3: 332.
- Gude, G.K. (1897f): Armature of Helicoid landshells, With a new species of *Plectopylis*. *Science Gossip*, 4: 10–11.
- Gude, G.K. (1897g): Armature of Helicoid landshells. With a new form of *Plectopylis*. *Science Gossip*, 4: 36–37.
- Gude, G.K. (1897h): Armature of Helicoid landshells, With new species of *Plectopylis*. *Science Gossip*, 4, 70–71.
- Gude, G.K. (1897i): Armature of Helicoid landshells. *Science Gossip*, 4: 102–103.
- Gude, G.K. (1897j): Armature of Helicoid landshells. *Science Gossip*, 4: 138–139.
- Gude, G.K. (1897k): Armature of Helicoid landshells, With new species of *Plectopylis*. *Science Gossip*, 4: 170–171.
- Gude, G.K. (1897l): Species of *Plectopylis* recently described in “Science Gossip.” *The Journal of Malacology*, 6: 44–48.
- Gude, G.K. (1898a): Armature of Helicoid landshells With New Species of *Plectopylis*. *Science Gossip*, 4: 231–232.
- Gude, G.K. (1898b): Armature of Helicoid landshells, With a New Species of *Plectopylis*. *Science Gossip*, 4: 263–264.
- Gude, G.K. (1898c): Armature of Helicoid landshells With a new form of *Plectopylis*. *Science Gossip*, 4: 284–285.
- Gude, G.K. (1898d): Armature of Helicoid landshells. *Science Gossip*, 5: 15–17.
- Gude, G.K. (1898e): Armature of Helicoid landshells. *Science Gossip*, 5: 74–76.

- Gude, G.K. (1898f): Armature of Helicoid landshells. And New Forms of *Plectopylis*. *Science Gossip*, 5: 114–115.
- Gude, G.K. (1898g): Armature of Helicoid landshells. And New Forms of *Plectopylis*. *Science Gossip*, 5: 133–134.
- Gude, G.K. (1898h): Armature of Helicoid landshells. And New Forms of *Plectopylis*. *Science Gossip*, 5: 170–172.
- Gude, G.K. (1898i): Species of *Plectopylis* recently described in “Science Gossip.” *The Journal of Malacology*, 7: 7–16.
- Gude, G.K. (1899a): Armature of Helicoid landshells. And a new species of *Plectopylis*. *Science Gossip*, 5: 239–240.
- Gude, G.K. (1899b): Armature of Helicoid landshells. And new forms of *Plectopylis*. *Science Gossip*, 5: 332–333.
- Gude, G.K. (1899c): Armature of Helicoid landshells. And a new species of *Plectopylis*. *Science Gossip*, 6: 15–17.
- Gude, G.K. (1899d): Armature of Helicoid landshells. And new species of *Plectopylis*. *Science Gossip*, 6: 75–77.
- Gude, G.K. (1899e): Armature of Helicoid landshells and new sections of *Plectopylis*. *Science Gossip*, 6: 147–149.
- Gude, G.K. (1899f): Armature of Helicoid landshells. *Science Gossip*, 6: 174–177.
- Gude, G.K. (1900a): Description of a new species of *Plectopylis* from Tonkin. *The Annals and Magazine of Natural History*, 7 (5): 313.
- Gude, G.K. (1900b): Species of *Plectopylis* recently described in “Science Gossip.” *The Journal of Malacology*, 7: 34–38.
- Gude, G.K. (1900c): Notes on some Specimens of *Plectopylis*. *The Journal of Malacology*, 7: 91.
- Gude, G.K. (1901a): On two new and three hitherto unfigured species of *Plectopylis* from Tonkin. *Journal of Malacology*, 8: 110–117.
- Gude, G.K. (1901b): Sur une collection de *Plectopylis* du Tonkin, avec la description de six espèces nouvelles. *Journal de Conchyliologie*, 49: 197–212.
- Gude, G.K. (1901c): Notes on some known species of *Plectopylis*, and description of a new variety of *Plectopylis plectostoma*, Bens. *The Journal of Malacology*, 8: 47–49.
- Gude, G.K. (1908a): On the identity of *Plectopylis leiophis* and *P. pseudophis*. *Proceedings of the Malacological Society of London*, 8: 88–89.
- Gude, G.K. (1908b): 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, G.K. (1909): Descriptions of six new species of *Plectopylis* from Tonkin. *Proceedings of the Malacological Society of London*, 8 (4): 213–218.
- Gude, G.K. (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.
- Gude, G.K. (1914a): Descriptions of new species of helicoids from the Indian Region. *Proceedings of the Malacological Society of London*. 11 (1): 52–57.
- Gude, G.K. (1914b): The Fauna of British India including Ceylon and Burma. Mollusca.–II. (Trochomorphidae--Janellidae). 1–520., London (Taylor and Francis).
- Gude, G.K. (1915): XL. Mollusca: IV: Helicidae. Genus *Plectopylis*. *Records of the Indian Museum*, 8: 505–513.
- Gude, G.K. (1920): Presidential address. The armature of land Mollusca. *Journal of Molluscan Studies*, 14 (2–3): 52–73.
- Haas, F. (1933): Zur Systematik der chinesischen “Helicodonten”. *Archiv für Molluskenkunde*, 65 (4/5): 230–231.
- Haas, F. (1945): Malacological Notes IV. *Fieldiana Zoology* 31 (2): 3–14.
- Haas, F. (1949): Land and fresh-water Mollusks from Peru. *Fieldiana Zoology* 31 (28): 235–250.
- Hanley, S.C.T. & Theobald, W. (1870–1876): *Conchologia Indica*; Being Illustrations of the Land and Freshwater Shells of British India. I–CLX, 1–65; London (L. Reeve & Co.).
- Harris, D.J. & Froufe, E. (2005): Taxonomic inflation: species concept or historical geopolitical bias? *TRENDS in Ecology and Evolution* 20: 6–7.
- Hausdorf, B. (2003): Systematic position and taxonomy of the genus *Hirtudiscus* from Colombia (Gastropoda: Scolodontidae). *Journal of Molluscan Studies* 69: 179–186.
- Hausdorf, B. (2006): The Systematic Position of *Scolodonta* Döring, 1875 and Scolodontidae H. B. Baker, 1925 (Gastropoda: Pulmonata). *Zoologischer Anzeiger*, 245 (3/4): 161–165.
- Hausdorf, B. (2011), Progress toward a general species concept. *Evolution*, 65: 923–931.
- Hawliczek, O., Nagy, Z.T. & Glaw, F. (2012): Island Evolution and Systematic Revision of Comoran Snakes: Why and When Subspecies Still Make Sense. *PLoS ONE* 7(8): e42970. doi:10.1371/journal.pone.0042970

- Hemmen, J. & Hemmen, C. (2001): Aktualisierte Liste der Terrestrischen Gastropoden Thailands. *Schriften zur Malakozoologie*, 18, 35–70.
- Hennig W. 1966. Phylogenetic Systematics. Urbana, IL: University of Illinois Press.
- Heude, R.P.M. (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, 1–88; Chang-Hai (Mission Catholique).
- Heude, R.P.M. (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, 89–132; Chang-Hai (Mission Catholique).
- Heude, R.P.M. (1889a): Diagnoses Molluscorum novorum in Sinis collectorum. *Journal de Conchyliologie*, 37: 40–50.
- Heude, R.P.M. (1889b): Diagnoses Molluscorum novorum in Sinis collectorum (Ex provincia Kouang-si). *Journal de Conchyliologie*, 37: 225–229.
- Heude, R.P.M. (1890): 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. IV, 125–188; Chang-Hai (Mission Catholique).
- Hoo, W.H. (1996): Conservation of Hong Kong land snails. *Tentacle*, 6: 12–14.
- Hrubesch, K. (1965): Die santone Landschneckenfauna von Glanegg bei Salzburg, Österreich. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historischen Geologie*, 5: 83–120.
- Hylton Scott, M.I. (1973): Endodontidos neotropicales V (Gastropoda Pulmonata). *Neotropica*, 19: 126–131.
- Hu, Z., Yin, H. & Chen, D. (2004): 南嶺國家森林公園的陸生貝類 (Terrestrial Mollusca of the Nanling National Park). *Journal of Natural Science of Hunan Normal University*, 27 (2): 67–70.
- Hwang, C.C., Wu, S.P., Ohara, K., Otani, Y & Otani, J.U. (2008): Further land snail types collected from Taiwan and deposited in the Nishinomiya Shell Museum. *Venus* 67 (1–2): 53–60.
- Isaac, N.J.B., Mallet, J. & Mace, G.M. (2004): Taxonomic inflation: its influence on macroecology and conservation. *TRENDS in Ecology and Evolution* 19: 464–469.
- Jaekel, S.H. (1950): Die Mollusken eines tropischen Flußgenistes aus Tonkin. *Archiv für Molluskenkunde*, 79: 15–20.
- Jaekel, S.H. (1950): Die Mollusken eines tropischen Flußgenistes aus Tonkin. *Archiv für Molluskenkunde*, 79: 15–20.
- Johnson, R.I. (1964): The recent Mollusca of Augustus Addison Gould. Smithsonian Institution, Washington DC 239:v + 182.
- Johnson, R.J. (1973): Heude's Molluscan Types: or, Asian land and fresh water mollusks, mostly from the People's Republic of China, described by P. M. Heude. Cambridge, Massachusetts (Special Occasional Publication, Department of Mollusks, Museum of Comparative Zoology, Harvard University), 1–111.
- Joppa, L.N., Roberts, D.L. & Pimm, S.L. (2011): The population ecology and social behaviour of taxonomists. *Trends Ecol. Evol.* 26, 551–553.
- Kerney, M.P. & Cameron, R.A.D. (1979): A Field Guide to the Land Snails of Britain and North-west Europe. 1–288; London (Collins).
- Kim, K.C. & Byrne, L.B. (2006): Biodiversity loss and the taxonomic bottleneck: emerging biodiversity science. *Ecol Res* 21: 794–810.
- Kimura, K., Chiba, S. & Koene, J.M. (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.
- Knapp, S., Lughadha, E.N. & Paton, A. (2005): Taxonomic inflation, species concepts and global species lists. *TRENDS in Ecology and Evolution* 20: 7–8.
- Kobelt, W. (1879): *Illustriertes Conchylienbuch*. Nürnberg, Bauer & Raspe, 2: 392 pp., Plates 51–112.
- Koene, J.M. & Chase, R. (1998): The love dart of *Helix aspersa* Müller is not a gift of calcium. *Journal of Molluscan Studies* 64: 75–80.
- Köhler, F. (1988): Amateurwissenschaft: Entwicklung, Beschreibung und wissenschaftssoziologische Analyse am Beispiel der Koleopterologie p. 195 (Diploma thesis: Sociology, Univ. Köln).
- Krell, F.-T. (2000): Impact factors aren't relevant to taxonomy. *Nature*, 405, 507–508.

- Krell, F.-T. (2002): Why impact factors don't work for taxonomy. *Nature*, 415, 957–957.
<http://dx.doi.org/10.1038/415957a>
- 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.
- La Salle, J., Wheeler, Q., Jackway, P., Winterton, S., Hobern, D. & Lovell, D. (2009): Accelerating taxonomic discovery through automated character extraction. *Zootaxa*, 2217 2217: 43–55.
- Laurin, M. (2010): The subjective nature of Linnaean categories and its impact in evolutionary biology and biodiversity studies. *Contributions to Zoology*, 79 (4): 131–146.
- Li, Y.-T. (1984): Early Tertiary Non-Marine gastropods from Lingbao Basin of Henan Province. *Professional Papers of Stratigraphy and Palaeontology*, 11: 1–30.
- Li, Y.-T. (1985): 山东昌乐五图组的非海栖腹足类化石. *Professional Papers of Stratigraphy and Palaeontology*, 12: 237–250.
- Li, Y.-T. (1986): The correction of diagnosis and classification of the gastropod *Plectopyloides* Yen. *Professional Papers of Stratigraphy and Palaeontology*, 14: 241–252.
- Lydeard, C., Cowie, R.H., Ponder, W.F., Bogan, A.E., Bouchet, P., Clark, S.A., Cummings, K.S., Frest, T.J., Gargominy, O., Herbert, D.G., Herschler, R., Perez, K.E., Roth, B., Seddon, M., Strong, E.E. & Thompson, F.G. (2004): The Global Decline of Nonmarine Mollusks. *Bioscience* 54(4): 321–330.
- Maassen, W.J.M., (2001): A preliminary checklist of the non-marine Molluscs of West-Malaysia. “A handlist”. *De Kreukel, Extra Editie [for 2001]*: 1–155.
- Maassen W.J.M. & Gittenberger, E. (2007): Three new clausiliid land snails from Tonkin, northern Vietnam (Gastropoda: Pulmonata: Clausiliidae). *Zool. Med. Leiden* 81 (10): 175–186.
- Mabille, M.J. (1887a May): *Molluscorum Tonkinorum diagnoses*: 18 pp; Paris (Masson).
- Mabille, M.J. (1887b July): *Sur Quelques Mollusques du Tonkin*. *Bulletins de la Société Malacologique de France*, 4: 73–164.
- Mallet, J., Isaac, N.J.B. & Mace, G.M. (2005): Response to Harris and Froufe, and Knapp et al.: Taxonomic inflation. *TRENDS in Ecology and Evolution* 20: 8–9.
- Manganelli, G., Delle Cave, L. & Giusti, F. (1989): *Notulae malacologicae*, XLII. Strobilopsidae (Gastropoda, Pulmonata), a family new to the Villafranchian land snail fauna of Appenninic Italy. *Basteria*, 53: 3–13.
- Manganelli, G., Aldinucci, M., Capezzuoli, E. & Benocci, A. (2008): Strobilopsid land snails (Gastropoda: Pulmonata, Strobilopsidae) from the late Messinian - Early Pliocene (?) of Balze di Caspreno (central Italy). *Bollettino della Società Paleontologica Italiana*, 46 (2–3): 101–106.
- Manier, M.K. (2004): Geographic variation in the long-nosed snake, *Rhinocheilus lecontei* (Colubridae): beyond the subspecies debate. *Biol J Linn Soc* 83: 65–85.
- Martens, E. von (1867): *Die Preussische Expedition Nach Ost-Asien*. Nach Amtlichen Quellen. Zoologischer Theil. Zweiter Band. Die Landschnecken. 1–447; Berlin (Verlag der Königlichen Geheimen Ober-Hofbuchdruckerei).
- Martens, E. v. (1868): *Ueber einige Heliceen vom Himalaya*. *Malakozoologische Blätter* 15: 157–162.
- Martens, E. von (1875a): *Bemerkungen zu vorstehender Arbeit*. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 2: 126–135.
- Martens, E. von (1875b): *Einige neue ostasiatische Land- und Süßwasser-Conchylien*. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin*: 2–4.
- Maupas, E. (1899): *La mue et l'enkystement chez les nématodes*. *Archives de Zoologie et Expérimentale (3e. Série)* 7: 563–628.
- May, R. (2010): Tropical arthropod species, more or less? *Science* 329: 41–42.
- Mayr, E. (1942): *Systematics and the origin of species*. New York (Columbia Univ. Press).
- McGhie, H.A. (2008): *Catalogue of type specimens of molluscs in the collection of The Manchester Museum, The University of Manchester, UK*. *Zookeys* 4: 1–46.
- McHugh, D. (1997): Molecular evidence that echiurans and pogonophorans are derived annelids. *Proceedings of the National Academy of Sciences of the United States of America* 94: 8006–8009.
- McMichael, D.F. (1959): A new genus and species of land snail from North Queensland. *Journal of the Malacological Society of Australia* 3: 31–32.

- Michener, C.D., Corliss, J.O., Cowan, R.S., Raven, P.H., Sabrosky, C.W., Squires, D.S. & Wharton, G.W. (1970): Systematics In Support of Biological Research. Division of Biology and Agriculture, National Research Council. Washington, D.C. 25 pp.
- Miller, S.E. (2007): DNA barcoding and the renaissance of taxonomy. *Proc. Natl Acad. Sci. USA* 104, 4775–4776.
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011): How Many Species Are There on Earth and in the Ocean? *PLOS Biology* 9(8): e1001127. doi:10.1371/journal.pbio.1001127
- Morlet, L. (1886a): Liste des Conquilles recueillies, au Tonkin, par M. Jourdy, chef d'escadron d'artillerie, et description d'espèces nouvelles. *Journal de Conchyliologie*, 34: 257–295.
- Morlet, L. (1886b): Diagnoses de mollusques terrestres et fluviatiles du Tonkin. 1–7.
- Möllendorff, O. F. von (1882): Diagnoses specierum novarum Chinae meridionalis. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 9: 179–188.
- Möllendorff, O. F. von (1883): Materialien zur Fauna for China. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 10: 356–383.
- Möllendorff, O. F. von (1885a): Materialien zur Fauna for China. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 12: 349–398.
- Möllendorff, O. F. von (1885b): Diagnoses specierum novarum sinensium. *Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft*, 11–12: 161–170.
- Möllendorff, O. F. von (1886): Materialien zur Fauna for China. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft*, 13: 156–210.
- Möllendorff, O. von (1897): Drei neue Arten. *Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft*, 29, 28–31.
- Möllendorff, O. F. von (1898): Verzeichniss der auf den Philippinen lebenden Landmollusken. *Abhandlungen der Naturforschenden Gesellschaft zu Görlitz* 22: 25–208.
- Möllendorff, O. von (1901a): Diagnosen neuer von H. Fruhstorfer in Tongking gesammelter Landschnecken. *Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft*, 33 (5/6): 65–81.
- Möllendorff, O. von (1901b): Diagnosen neuer von H. Fruhstorfer in Tongking gesammelter Landschnecken. *Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft*, 33 (5/6): 110–119.
- Möllendorff, O. F. von (1902): Binnen-Mollusken aus Westchina und Central-Asien II. Nach den Sammlungen von Przewalski, Potanin, Beresowski, Gnum-GRSHIMAILO u. a. im Zoologischen Museum der Kaiserl. Akademie der Wissenschaften zu St. Petersburg. 114 pp. (300–412), 12–17 plates; Sanktpeterburg (*Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Petersbourg*).
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000): Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Neubert, E. (2014): Revision of *Helix* Linnaeus, 1758 in its eastern Mediterranean distribution area, and reassignment of *Helix godetiana* Kobelt, 1878 to *Maltzanella* Hesse, 1917. *Contributions to Natural History*, vol. 26: 1–200.
- Nevill, G. (1877): List of the Mollusca brought back to Mr. Anderson from Yunnan and upper Burma with descriptions of new species. *Journal of the Asiatic Society of Bengal*, 46: 14–41.
- Nevill, G. (1878a): Hand list of Mollusca in the Indian Museum, Calcutta. Part I. Gastropoda. Pulmonata and Prosobranchia-Neurobranchia. 1–338; Calcutta (Order of the Trustees).
- Nevill, G. (1878b): Mollusca. In: Anderson, J. (ed.), *Anatomical and Zoological Researches Comprising an Account of the Zoological Results of the Two Expeditions to Western Yunnan in 1868 and 1875*, 1–985; London (Quaritch).
- Nevill, G. (1881): New or little-known Mollusca of the Indo-Malayan fauna. *Journal of the Asiatic Society of Bengal*, 50 (2): 125–167, pls. 5–7.
- Niknejad, A., Comte, A., Parmentier, G., Roux, J., Bastian, F.B. & Robinson-Rechavi, M. (2012): vHOG, a multispecies vertebrate ontology of homologous organs groups. *Bioinformatics* 28: 1017–1020.
- Nilsson, R.H., Ryberg, M., Kristiansson, E., Abarenkov, K., Larsson, K.-H., Kõljalg, U. (2006): Taxonomic Reliability of DNA Sequences in Public Sequence Databases: A Fungal Perspective. *PLoS ONE* 1(1): e59. doi:10.1371/journal.pone.0000059
- Nixon, K.C. & Wheeler, Q.D. (1990): An amplification of the phylogenetic species concept. *Cladistics* 6: 211–223.

- Nordsieck, H. (1982): Die Evolution des Verschlußapparats der Schließmundschnecken (Gastropoda: Clausiliidae). – Archiv für Molluskenkunde, 112 (1/6): 27–43.
- Nordsieck, H. (1986): The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae II. Importance of the shell and distribution. Archiv für Molluskenkunde, 117 (1/3): 93–116.
- Nordsieck, H. (2001): Revision of the system of the Phaedusinae from mainland China with the description of new taxa (Gastropoda: Stylommatophora: Clausiliidae). Archiv für Molluskenkunde, 129 (1/2): 25–63.
- Nordsieck, H. (2007): Worldwide Door Snails (Clausiliidae), recent and fossil. Hackenheim.
- Nordsieck, H. (2011): Clausiliidae of Vietnam with the description of new taxa (Gastropoda: Stylommatophora). Archiv für Molluskenkunde, 140 (2): 149–173.
- Oppenheim, P. (1892): Ueber einige Brackwasser- und Binnenmollusken aus der Kreide und dem Eocän Ungarns. Zeitschrift der Deutschen Geologischen Gesellschaft 44: 697–818.
- Padial, J.M. & De la Riva, I. (2007): Taxonomy, the Cinderella of science, hidden by its evolutionary stepsister. Zootaxa 1577, 1–2.
- Páll-Gergely, B. (2010): Additional information on the reproductive biology and development of the clausilial apparatus in *Pontophaedusa funiculum* (Mousson 1856) (Gastropoda, Pulmonata, Clausiliidae, Phaedusinae). Malacologica Bohemoslovaca 9: 1–4.
- Páll-Gergely, B. (2014): Suggestions to improve the Taxonomy Index (T-Index) introduced by Valdecasas (2011). Zootaxa, 3780 (2), 399–400.
- Páll-Gergely, B. (2015): On the confusion of quality with impact: A note on Pyke's (2014) M-Index. — Bioscience, 65 (2): 117.
- Páll-Gergely, B. & Hunyadi, A. (2013): The family Plectopylidae Möllendorff 1898 in China (Gastropoda, Pulmonata). Archiv für Molluskenkunde 142 (1): 1–66.
- 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.
- Páll-Gergely, B., Hunyadi, A., Ablett, J., Luong Van, H., Naggs, F. & Asami, T. (2015): Systematics of the family Plectopylidae in Vietnam with additional information on Chinese taxa (Gastropoda, Pulmonata, Stylommatophora). — Zookeys 472: 1–118.
- Pfeiffer, L. (1845): Uebersicht der mit inner Lamellen versehenen Helix-Arten. Zeitschrift für Malakozoologie, 2: 81–87.
- Pfeiffer, L. (1848): Die Schnirkelschnecken (Gattung *Helix*.) In Abbildungen nach der Natur mit Beschreibungen. In: Martini & Chemnitz: Systematisches Conchylien-Cabinet, 1(12): 400 pp, 66 plates. Nürnberg, Bauer & Raspe.
- Pfeiffer, L. (1853): Monographia heliceorum viventium. Sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum. Volumen tertium. - pp. I–VIII [= 1–8], 1–711. Lipsiae. (Brockhaus).
- Pfeiffer, L. (1862): Description of Thirty-six New Land Shells From the Collection of H. Cuming, Esq. Proceedings of the Zoological Society of London, 268–278.
- Pfeiffer, L. (1863): Novitates Conchologicae, Series prima. Mollusca extramarina. Descriptions et figures de coquilles, estramarines nouvelle, ou peu connues. Beschreibung und Abbildung neuer oder kritischer Land- und Süßwasser Mollusken. Cassel, Germany: T. Fischer. 2: 139–303.
- Pfeiffer, L. (1867): Eine neue *Helix*. *Malakologische Blätter*, 14: 64.
- Pfeiffer, L. (1868): Monographia Heliceorum Viventium: Sistens Descriptiones Systematicas et Criticas Omnium Huius Familiae Generum et Specierum Hodie Cognitarum. V: 1–565; Lipsia (Brockhaus).
- Pfeiffer, L. (1869): Novitates conchologicae. Series prima. Mollusca extramarina. Beschreiber und Abbildung, neuer oder kritischer Land- und Süßwasser-Mollusken. (Mit Einschluss der Auricularceen). Band 3. Cassel, Theodor Fischer.
- Pfeiffer, L. (1876a): Monographia Heliceorum Viventium. Sistens Descriptiones Systematicas et Criticas Omnium Huius Familiae Generum et Specierum Hodie Cognitarum. VII: 1–674; Lipsia (Brockhaus).
- Pfeiffer, L. (1876b): Bemerkungen zum achten Bande meiner Monographia Heliceorum. *Malakozoologische Blätter*, 23: 196–230.

- Pfeiffer, L. (1878): Nomenclator heliceorum viventium quo continetur nomina omnium hujus familiae generum et specierum hodie cognitarum, disposita ex affinitate naturali. Opus postumum Ludovici Pfeiffer ed. S. Clessin. pp. 617. Cassellis. (Fischer).
- Pfeiffer, L. & Clessin, S. (1881): Nomenclator Heliceorum viventium quo continetur nomina omnium hujus familiae generum et specierum hodie cognitarum, disposita ex affinitate naturali. 1–617; Cassellis (Sumptibus Theodori Fischer).
- Philippi, R.A. (1847): Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien. 3, 138 pp, Theodor Fischer, Cassel.
- Phillips, J. (1845): On the Remains of Microscopic Animals in the Rocks of Yorkshire. Proceedings of the Yorkshire Geological and Polytechnic Society, 2: 274–285.
- Phillimore, A.B. & Owens, I.P.F. (2006): Are subspecies useful in evolutionary and conservation biology? P R Soc B 273: 1049–1053.
- Pilsbry, H.A. (1893): Manual of Conchology; Structural and Systematic. With illustrations of the Species. Second series: Pulmonata. Vol. 8., I–LVIII, 1–297; Philadelphia (Conchological Section, Academy of Natural Sciences).
- Pilsbry, H.A. (1894–1895): Manual of Conchology. Second Series: Pulmonata. Vol. 9: 49–336; Philadelphia (Academy of Natural Sciences Philadelphia).
- Pilsbry, H.A. (1896): The Aulacopoda: A Primary division of the Monotremate land Pulmonata. The Nautilus 9: 109–111.
- Pilsbry, H.A. (1904): *Plectopylis* in the Riukiu Islands. Nautilus, 18: 58–59.
- Pilsbry, H.A. (1905): Anatomical and systematic notes on *Dorcasia*, *Trigonephrus*, n. gen., *Corilla*, *Thersites*, and *Chloritis*. Proceedings of the Malacological Society of London 6: 286–291.
- Pilsbry H.A. (1927): Manual of Conchology, structural and systematic, with illustrations of the species. Second series: Pulmonata. Volume 28. Geographic Distribution of Pupillidae; Strobilopsidae, Valloniidae and Pleurodiscidae. Conchological department Academy of Natural Sciences of Philadelphia, Philadelphia. 1–48.
- Pilsbry, H.A. (1930): Anatomy and relationships of some American Helicidae and Polygyridae. Proceedings of the Academy of Natural Sciences of Philadelphia 82: 303–327.
- Ponder, W., Hutchings, P. & Chapman, R. (2002): Overview of the Conservation of Australian Marine Invertebrates. Canberra: Environment Australia. http://www.amonline.net.au/invertebrates/marine_overview/index.html
- Porro, C. (1836): Drépanostome. Drepanostoma. Magasin de Zoologie 6 (Cl. V Pl. 71): 1–2, Pl. 71.
- Potiez, V.-L.-V. & Michaud, A.-L.-G. (1838): Galerie des mollusques, ou catalogue méthodique, descriptif et raisonné des mollusques et coquilles du Muséum de Douai. Tome premier. pp. I–XXXVI [= 1–36], 1–560, [1–4], atlas 1–56, Pl. I–XXXVII [= 1–37]. Paris, Londres. (Bailliére).
- Pyke, G.H (2014): Evaluating the Quality of Taxonomic Publications: A Simple Alternative to Citations and Effort. BioScience (2014). doi: 10.1093/biosci/biu154
- Qian, Z.-X., Zhang, W.-H., Guo, Y.-H. & Chen, D.-N. (2006): Terrestrial Mollusc Fauna and Ecological Distribution in Zhejiang Province. Sichuan Journal of Zoology, 25 (4): 814–818.
- Quadrás, J. F. & Moellendorff, O. F. von (1894): Diagnoses specierum novarum ex insulis Philippinis. Nachrichtenblatt der Deutschen Malakozoologischen Gesellschaft, 26: 113–130.
- Raheem, D. & Naggs, F. (2006): The Sri Lankan endemic semi-slug *Ratnadvipia* (Limacoidea: Ariophantidae) and a new species from southwestern Sri Lanka. *Systematics and Biodiversity*, 4, 99–126.
- Raheem, D. C., Taylor, H., Ablett, J., Preece, R. C., Aravind, N. A. & Naggs, F. (2014): A Systematic Revision of the Land Snails of the Western Ghats of India. Tropical Natural History Supplement 4: i–xiii, 1–285.
- Ramírez, R. (1993): A generic analysis of of the family Systrophiidae (Mollusca: Gastropoda): Taxonomy, Phylogeny and Biogeography. Magister Thesis, Austin, United States: University of Texas.
- Ramírez, R., Borda, V., Romero, P., Ramirez, J., Congrains, C., Chirinos, J., Ramírez, P., Velásquez, L.E. & Mejía, K. (2012): Biodiversity and endemism of the western Amazonia land snails *Megalobulimus* and *Systrophia*. Revista Peruana de Biología 19 (1): 59–74. (in Spanish)
- Reeve, L.A. (1854): Conchologia iconica, or, Illustrations of the shells of molluscous animals, Vol 7, (1495 species), 210 plates, London.

- Remane, A. (1952): Die Grundlagen Des Natürlichen Systems, der Vergleichenden Anatomie und der Phylogenetik. Leipzig: Akademische Verlagsgesellschaft.
- Remsen, J.V. (2010): Subspecies as a meaningful taxonomic rank in avian classification. *Ornith Mon* 67: 62–78.
- Richardson, L. (1986): Polygyracea: Catalog of species (Parts 1, Polygyridae; 2, Corillidae; 3, Sagdidae). *Tryonia Miscellaneous Publications of the Department of Malacology of the Academy of Natural Sciences of Philadelphia*, 13: 1–139.
- Ride W.D.L., Cogger, H.G., Dupuis, C., Kraus, O., Minelli, A., Thompson, F.C. & Tubbs, P.K. (1999): International Code of Zoological Nomenclature. Fourth edition adopted by the International Union of Biological Sciences. Code International de Nomenclature Zoologique. Quatrième édition. International Trust for Zoological Nomenclature, London.
- Riedel, A. & Urbański, J. (1964): Systematische Stellung und Angaben über das Vorkommen von *Paraegopsis* (*Balcanodiscus* subg. nov.) *frivaldskyanus* (Rossmässler 1842) (Gastropoda: Zonitidae). *Annales Zoologici*, 22 (4): 69–79.
- Rieppel, O. & Kearney, M. (2002): Similarity. *Biological Journal of Linnean Society* 75: 59–82.
- Sastry, M.V.A., Rao, B.R.J. & Mangain, V.D. (1968): Biostratigraphic zonation of the Upper Cretaceous formations of Trichinopoly District, South India. *Geological Society of India, Memoir* 2: 10–17.
- Saurin, E. (1953): Coquilles nouvelles de l'Indochine. *Journal de Conchyliologie*, 93 (4), 113–120.
- Scheffers, B.R., Joppa, L.N., Pimm, S.L. & Laurance, W.F. (2012): What we know and don't know about Earth's missing biodiversity. *Trends in Ecology and Evolution* 27, 501–510.
- Schileyko, A.A. (1998): Treatise on Recent Terrestrial Pulmonate Molluscs, Part 1. Achatinellidae, Amastridae, Orculidae, Strobilopsidae, Spelaeodiscidae, Valloniidae, Cochlicopidae, Pupillidae, Chondrinidae, Pyramidulidae. *Ruthenica, Supplement 2* (1): 1–127.
- Schileyko, A.A. (1999): Treatise on Recent Terrestrial Pulmonate Molluscs, Part 4. Draparnaudiidae, Caryodidae, Macrocyclidae, Acavidae, Clavatoridae, Dorcasiidae, Sculpitariidae, Corillidae, Plectopylidae, Megalobulimulidae, Strophocheilidae, Cerionidae, Achatinidae, Subulinidae, Glessulidae, Micractaeonidae, Ferrussaciidae. *Ruthenica, Supplement 2*: 435–564.
- Schileyko A.A. (2000): Treatise on recent terrestrial pulmonate molluscs: Rhytididae, Chlamydephoridae, Systrophiidae, Haplotrematidae, Streptaxidae, Spiraxidae, Oleacinidae, Testacellidae. *Ruthenica, Suppl. 2, Part 6*: 731–880.
- Schileyko, A.A. (2001): Treatise on Recent Terrestrial Pulmonate Molluscs, Part 7. Endodontidae, Thyrophorellidae, Charopidae. *Ruthenica, Supplement 2*: 881–1034.
- Schileyko, A.A. (2002): Treatise on recent terrestrial pulmonate molluscs. Part 8. Punctidae, Helicodiscidae, Discidae, Cystopeltidae, Euconulidae, Trochomorphidae. *Ruthenica, Supplement, 2* (8): 1035–1166.
- Schileyko, A.A. (2003a): Treatise on Recent terrestrial pulmonate molluscs. Part 11. Trigonochlamydidae, Papillodermidae, Vitrinidae, Limacidae, Bielziidae, Agriolimacidae, Boettgerillidae, Camaenidae. – *Ruthenica, suppl. 2*: 1467–1626.
- Schileyko, A.A. (2003b): Treatise on recent terrestrial pulmonate molluscs. 10. Ariophantidae, Ostracolethidae, Rysotidae, Milacidae, Dyakiidae, Staffordiidae, Gastrodontidae, Zonitidae, Daudebardiidae, Parmacellidae. *Ruthenica, Supplement 2*. 1309–1466.
- Schileyko, A.A. (2006a): Treatise on recent terrestrial pulmonate molluscs, Part 13. Helicidae, Pleurodontidae, Polygyridae, Ammonitellidae, Oreohelicidae, Thysanophoridae. *Ruthenica Supplement 2* (10): 1765–1906.
- Schileyko, A.A. (2006b): *Treatise on Recent terrestrial pulmonate molluscs, Part 14 Helicodontidae, Ciliellidae, Hygromiidae*. *Ruthenica, Supplement 2* (14): 1907–2047
- Schileyko, A.A. (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.
- Schileyko, A.A. (2011): Check-list of land pulmonate molluscs of Vietnam (Gastropoda: Stylommatophora). *Ruthenica*, 21 (1): 1–68.
- Schmacker, B. & Boettger, O. (1890): Neue Materialien zur Charakteristik und geographischen Verbreitung Chinesischer und Japanischer Binnenmollusken I. Mitteilungen aus der Gebiete der Malakozoologie, 1–2: 1–30.

- Sefrova, H. & Lastuvka, Z. (2001): Dispersal of the horse-chestnut leafminer, *Cameraria ohridella* Deschka & Dimic, 1986, in Europe: its course, ways and causes (Lepidoptera: Gracillariidae). *Entomologische Zeitschrift – Stuttgart* 111: 194–198.
- Smith, B. & Stanisci, J. (1998): Pulmonata. In *Mollusca: The Southern Synthesis. Fauna of Australia*. (Eds PL Beesley, GJB Ross and A Wells) pp. 1037–1125.
- Sodhi, N.S., Koh, L.P., Brook, B.W. & Ng, P.K.L. (2004): Southeast Asian biodiversity: an impending disaster. *TRENDS in Ecology and Evolution* 19 (12): 654–660.
- Solem, A. (1957): Philippine snails of the family Endodontidae. *Fieldiana Zoology* 42 (1): 1–12.
- 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.
- Solem, A. (1979): Biogeographic significance of land snails, paleozoic to recent. In: Gray J, Boucot A.J, editors. *Historical biogeography, plate tectonics, and the changing environment*. Oregon State University Press; Corvallis, OR: pp. 277–287.
- Solem, A. (1981): Land snail biogeography: a true snail's pace of change. Pp. 197–237, figs. 5.1–5.14. In: G. Nelson & D. E. Rosen (eds.), *Vicariance Biogeography: A Critique*. Columbia University Press: New York.
- Steinke, D., Albrecht, C. & Pfenninger, M. (2004): Molecular phylogeny and character evolution in the western Palaearctic Helicidae s.l. (Gastropoda: Stylommatophora). *Mol. Phyl. Evol.* 32, 724–734.
- Stoliczka, F. (1868): Cretaceous fauna of Southern India. II: Gastropoda. *Palaeontologica Indica*, being figures and descriptions of the organic remains procured during the progress of the Geological Survey of India. *Memoirs of the Geological Survey of India* 5, 1–498.
- 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.
- Stoliczka, F. (1873): Descriptions of two new species of Indian Landshells. *Journal of the Asiatic Society of Bengal*, 42 (2), 169–171.
- Su, X.-M., Li, D.-H. & Yang, W.-Ch. (2007): Animal community structure and its relations with environmental factors in Lianhua and Ziyang caves of Guizhou Province. *Chinese Journal of Ecology* 26 (12): 1981–1987.
- Sulikowska-Drozd, A. (2009): Development of clausiliar apparatus in *Vestia gulo* (E.A. Bielz, 1859) (Gastropoda: Pulmonata: Clausiliidae). – *Folia Malacologica*, 17(2): 77–80.
- Szekeres, M. (1998): The systematic position of the *Garnieria* and *Tripychia* groups, two ambiguous phylogenetic branches of Clausiliidae (Gastropoda Pulmonata). *Basteria* 62: 175–179.
- Tangley, L. (1997). How many species are there? *US News and World Report* Aug. 18, 1997. http://www.usnews.com/usnews/culture/articles/970818/archive_007681.htm
- Tapparone Canefri, T. (1889): Viaggio di Leonardo Fea in Birmania e regioni vicine. XVIII. – Molluschi terrestri e d'acqua dolce. *Annali del Museo Civico di Storia Naturale di Genova*, 2a (7): 295–359.
- Tausch, L. (1886): Ueber die Fauna der nicht marinen Ablagerungen der oberen Kreide des Csingerthales bei Ajka im Bakony (Veszprimer Comitatus, Ungarn). *Abhandlungen der K.u.K. Geologischen Reichsanstalt*, 12: 1–32.
- Templeton, A.R. 1989. The meaning of species and speciation. Pp. 3–27 in D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sinauer, Sunderland, MA.
- Thanh, Đ.N. (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).
- Theobald, W. (1857): Notes on the distribution of some land and freshwater shells of India: Part I. *Journal of the Asiatic Society of Bengal*, 26: 245–254.
- Thiele, J. (1926): Mollusca = Weichtiere. In: Kükenthal W, Krumbach T (Eds) *Handbuch der Zoologie*. Walter de Gruyter, Berlin and Leipzig, Vol.5, pp. 177–256.
- Tillier, S. (1980): Gastéropodes terrestres et fluviatiles de Guyane Française. *Mémoires du Muséum national d'Histoire naturelle, Série A, Zoologie* 118: 3–189.
- Tillier, S. (1989): Comparative morphology, phylogeny and classification of land snails and slugs (Gastropoda: Pulmonata: Stylommatophora). *Malacologia*, 30: 1–303.

- Tompa, A. (1984): Land snails (Stylommatophora). In: Wilbur KM (Ed.) The Mollusca, vol VII: Reproduction. Academic Press, London, pp 47–140.
- Tryon, G.W. (1887): Manual of Conchology; Structural and Systematic. With Illustrations of the Species. Second series: Pulmonata. Volume III. Helicidae, Volume I., 1–313. Philadelphia (Published by the Author).
- Tumpeesuwan, Ch. & Tumpeesuwan, S. (2010): Species Diversity and Abundance of Land Snails in Limestone and Sandstone Hills in Nong Bua Lamphu Province. *Burapha Science Journal*, 2: 10–19. (In Thai)
- Ueshima, R. & Asami, T. (2003): Single-gene speciation by left–right reversal. *Nature*, 425, 679.
- Valdecasas, A.G., Castroviejo, S. & Marcus, L.F. (2000): Reliance on the citation index undermines the study of biodiversity. *Nature*, 403, 698–698.
- Valdecasas, A.G. (2011): An index to evaluate the quality of taxonomic publications. *Zootaxa*, 2925, 57–62.
- Valdecasas, A.G. (2014): A reply to Páll-Gergely's suggestions to improve the taxonomy index (T-Index) introduced by Valdecasas (2011). *Zootaxa*, 3784 (1): 099–100.
- Venu, P. & Sanjappa, M. (2011): The impact factor and taxonomy. *Current Science* 101: 1397.
- Verdcourt, A. (1979): The identity of the European greenhouse *Gulella* (Pulmonata: Streptaxidae). *Journal of Conchology* 30: 101–104.
- Verdcourt, B. (1985): New taxa of *Gulella* L. PFR and *Ptychotrema* Mörch (Mollusca, Streptaxidae) from eastern Africa. *Journal of Conchology* 32: 109–121.
- Visser, M. (1973): The ontogeny of the reproductive system of *Gonaxis gwandaensis* (Preston) (Pulmonata, Streptaxidae) with special reference to the phylogeny of the spermatid conduits of the pulmonata. *Annals of the University of Stellenbosch, Seria A* 48(4): 1–79.
- Wade, C.M., Mordan, P.B. & Clarke, B. (2000): A phylogeny of the land snails (Gastropoda: Pulmonata). *Proceedings of the Royal Society of London, B* 268: 413–422.
- Wade, C.M., Mordan, P.B. & Naggs, F. (2006): Evolutionary relationships among the Pulmonate land snails and slugs (Pulmonata, Stylommatophora). *Biological Journal of the Linnean Society* 87: 593–610.
- Wade, C.M., Hudelot, C., Davison, A., Naggs, F. & Mordan, P.B. (2007): Molecular phylogeny of the helicoid land snails (Pulmonata: Stylommatophora: Helicoidea), with special emphasis on the Camaenidae. *Journal of Molluscan Studies* 73: 411–415.
- Wägele, H., Klusmann-Kolb, A., Kuhlmann, M., Haszprunar, G., Lindberg, D., Koch, A. & Wägele, J. (2011): The taxonomist - an endangered race. A practical proposal for its survival. *Frontiers in Zoology*, 8: 25.
- Weyrauch, W.K. (1960): Zwanzig neue Landschnecken aus Peru. *Archiv für Molluskenkunde* 89 (1/3): 23–48.
- Wheeler, Q. (2004): Taxonomic triage and the poverty of phylogeny. *Philosophical transactions of The Royal Society, London B, Biological Sciences* 359: 571–583.
- Wheeler, Q.D. (2008): Undisciplined thinking: morphology and Hennig's unfinished revolution. *Systematic Entomology* 33: 2–7.
- Wheeler, Q.D. (2014): Are reports of the death of taxonomy an exaggeration? *New Phytologist* (2014) 201: 370–371.
- Wheeler, Q.D. & Platnick, N.I. (2000): The phylogenetic species concept (sensu Wheeler and Platnick). In Wheeler QD, Meier R, editors. *Species Concepts and Phylogenetic Theory: A Debate*. New York: Columbia University Press. p 55–69.
- Wheeler, Q.D., Raven, P.H. & Wilson, E.O. (2004): Taxonomy: impediment or expedient? *Science* 303: 285.
- Wilkins, J.S. (2006). "Species, Kinds, and Evolution". *Reports of the National Center for Science Education*. 26 (4): 36–45.
- Wood, B. & Collard, M. (1999): The changing face of genus *Homo*. *Evolutionary Anthropology: Issues, News, and Reviews*, 8: 195–207.
- Wood, H. & Gallichan, J. (2008): The new Molluscan names of César-Marie-Felix ANCEY including illustrated type material from the National Museum of Wales. *Biotir Reports*, 3: 1–162.
- Woodward, B.B. (1925): Gerard Pierre Laurent Kalshoven Gude, F.Z.S., etc., 1858–1924. *Proceedings of the Malacological Society of London* 16(5): 205–206, pl. 9A.
- Wu, C.-I. 2001. The genic view of the process of speciation. *J. Evol. Biol.* 14:851–865.

- Yan, F., Zhang, L., Luo, T.-C. & Gu, X.-M. (2007): 3種陸生貝類不同組織酯酶(EST)同工酶比較分析 (The EST isozyme analysis on different tissues of three species of terrestrial mollusk). *Journal of Guizhou Normal University (Natural Sciences)*, 25 (3): 17–20. (In Chinese)
- Yen, T.-C. (1937): Notes on some gastropods of Hunan Province. *Bulletin du Musée royal d'Historie Naturelle de Belgique*, 13: 1–41.
- Yen, T.-C. (1939): Die Chinesischen Land-und Süßwasser-Gastropoden des Natur-Museums Senckenberg. 1–234, Frankfurt am Main (Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft).
- Yen, T.-C. (1941): A review of Chinese gastropods in the British Museum. *Proceeding of the Malacological Society of London*, 24: 170–289.
- Yen, T.-C. (1944): Notes on some unfigured type-specimens of Chinese Mollusks from the North Pacific Expedition. *Proceedings of the California Academy of Sciences*, 4th series, 23 (38): 561–586., Plates 50–51.
- Yen, T.-C. (1948): Notes in land and fresh-water mollusks on Chekiang Province, China. *Proceedings of the California Academy of Sciences*, 26 (4): 69–99.
- Yen, T.-C. (1969): Fossil nicht-marine Mollusken-Faunen aus Nordchina. *Sitzungsberichte der Österreichisch Akademie der Wissenschaften (Abt.I)*, 177: 55–57.
- Yu, W. & Pan, H.-Z. (1982): 河北涿县始新世非海相腹足类化石 (Eocene non-marine Gastropoda from Zhou Xian, Hebei). *Bulletin of Nanjing Institute of Geology and Paleontology, Academia Sinica*, 4: 189–212. (In Chinese).
- Zhouxing, Q. & Deniu, Ch. (2008): Farmland Molluscs from Zhejiang Province, China Prosobranchia ; (Archaeogastropoda , Mesogastropoda) Pulmonata ; (Stylommatophora). 1–425. (In Chinese)
- Zilch, A. (1959–1960): *Handbuch der Paleozoologie*, 6 (2) Euthyneura. 481–834; Berlin (Gebrüder Borntraeger).
- Zilch, A. (1967): Aus der Geschichte des Senckenberg-Museums. Nr 13. Geschichte der malakologischen Sektion. *Archiv für Molluskenkunde* 97: 7–43.
- Zilch, A. (1974): Vinzenz Gredler und die Erforschung der Weichtiere Chinas durch Franziskaner aus Tirol. *Archiv für Molluskenkunde*, 104: 171–228.