

On the shell and radular morphology of two endangered species of the genus *Margarya* Nevill, 1877 (Gastropoda: Viviparidae) from lakes of the Yunnan Plateau, Southwest China

FENGYUE SHU^{1,2,3} FRANK KÖHLER⁴ & HONGZHU WANG^{1*}

1 – State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

2 – Graduate School of Chinese Academy of Sciences, Beijing 100049, China

3 – College of Life Science, Qufu Normal University, Qufu 273165, China

4 – Australian Museum, 6 College St, Sydney NSW 2010, Australia

* Corresponding author: Email: wanghz@ihb.ac.cn.

Abstract

The viviparid genus *Margarya* Nevill, 1877 is endemic to China and has only been recorded from the lakes of the Yunnan Plateau. Currently, all recognized species of this genus have become threatened or even extinct due to water pollution and overharvesting. In the current paper, *Margarya melanioides* Nevill, 1877 and *Margarya mansuyi* Dautzenberg & Fischer, 1905 are re-described based on newly collected material from Lake Dianchi and Lake Xingyun respectively. Intraspecific morphological variability of the shell, especially with respect to the development of the spiral keel, was found to be great. *M. melanioides* and *M. mansuyi* can be easily distinguished from each other as well as from other congeners by their relative size, as well as the number and development of the spiral keels. Radulae of the two species are relatively uniform with little differentiation in the number and shape of the teeth.

Key words: Taxonomy, revision, freshwater, conservation, imperilment

Introduction

The genus *Margarya* was erected by Nevill (1877: 30) for the type species *M. melanioides* Nevill, 1877 based on its produced, ‘*Melania*’-like spire, a distinct suture, and prominent spiral keels (Nevill 1877). It is endemic to China, with a restricted distribution in the lakes of the Yunnan Plateau, such as Lakes Dianchi, Fuxian, Erhai, Yilong, Xingyun and Yangzong (Liu *et al.* 1995). According to Nevill (1877) and Tchang and Tsi (1949), species of *Margarya* differ from other viviparids by their relatively long, thick and stout shell, the presence of spiral keels, an obtuse apex, and scalariform whorls.

The taxonomic treatment at species-level has been confusing and the validity of most species has remained contentious for a long time due to their highly variable shell morphology. Tchang and Tsi (1949) revised the taxonomy of this genus and raised most subspecies or varieties to the species level. Seven species, including two new, and two new subspecies, were recognized as valid taxa – all of them showing a restricted distribution in Yunnan Province. Zhang (1986) assessed the rates of morphological variation within *M. melanioides* and *M. monodi* Dautzenberg & Fischer, 1905 and recognized four distinct shell types of the former and two shell types of the latter species. Subsequently, in a karyological study Chen *et al.* (1996) stated that *M. yaungtsunghaiensis* Tchang & Tsi, 1949 and *M. melanioides* differed from each other by having 12 and 9 pairs of chromosomes respectively. Since then, *Margarya* has remained largely unstudied. Currently, a total of eleven taxa are considered to represent valid species (Yen 1939, 1943; Tchang and Tsi 1949). Four of these species, *M.*

yaungtsunghaiensis, *M. elongata* Tchang & Tsi, 1949, *M. yini* Tchang & Tsi, 1949 and *M. tchangsii* Xia, 1982 have very restricted distributions and are endemic in a single lake, respectively. *M. yaungtsunghaiensis* occurs only in Lake Yangzonghai, while the latter three species occur in Lake Dianchi. *M. monodi*, *M. francheti* (Mabille, 1886) and *M. tropidophora* (Mabille, 1886) are found in two or three lakes, and the other four species, *M. melanioides*, *M. mansuyi* Dautzenberg & Fischer, 1905, *M. carinata* Neumayr, 1898 and *M. bicostata* Tchang & Tsi, 1949 have wider distributions in Yunnan and occur in a number of lakes (Liu and Wu 2005). However, the validity of most species-group taxa remains questionable since the original descriptions are usually not very detailed and relied mainly on shell features; some also included data on the radula morphology based on examination with the light microscope.

In 2007–2008, a survey of the freshwater molluscs of thirteen lakes with a surface area larger than 10 km² of the Yunnan-Guizhou Plateau was conducted by a triangular dredge and a weighted Petersen grab (1/16 m²). Living specimens of *M. melanioides* and *M. mansuyi* were collected only in Lake Dianchi and Lake Xingyun, and members of the genus were not found in other lakes in this survey. The decline and probable extinction of some species in the group are largely attributed to the integrated effects of habitat destruction, water pollution, overharvesting and overfishing. Since the 1980s, all those lakes have suffered serious deterioration due to urbanization and other anthropogenic activities. As a result, the diversity and population sizes of endemic species in these lakes have decreased continuously (Zhang *et al.* 1997; Cui *et al.* 2008).

In the present paper, we describe the shell and radular morphology of these two species. We also discuss their taxonomy and current conservation status.

Material and methods

Two surveys were conducted during November to December in 2007 and June to August in 2008. Five lakes (Lake Dianchi, Lake Fuxian, Lake Yangzonghai, Lake Xingyun and Lake Qilu) were sampled in the first survey, while all thirteen lakes were included in the second survey (Fig. 1). The studied lakes are small to medium-sized tectonic lakes with a maximum depth from 5 m to 150 m (Table 1). The substratum of those lakes is mainly silt, clay or sandy clay. Sampling sites were distributed uniformly in study lakes and covered all kinds of habitats. Molluscs were collected using a triangular dredge and a weighted Petersen grab (1/16 m²). The Petersen grab was used three times at each site. The triangular dredge (about 1 m in width and 0.5 cm in mesh

size) was used only in shallow water (less than 5 m), 1–2 sampling areas were selected according to previous records (Tchang and Tsi 1949; Zhang 1986; Chen *et al.* 1996) or suggestions of fisherman who had once caught *Margarya* species in the lakes, 10–20 samples were collected in each sampling area and 5–20 meters were dragged each time. When macrophytes occurred, in addition a modified dredge (1/5 m²) was used to collect epiphytic gastropods. Moreover, qualitative surveys were also conducted in the littoral zone (less than 0.5 m) with a pond-net (30 cm and 420 μm in diameter and mesh size, respectively), and 5–10 sites were sampled in each lake.

Specimens of *M. melanioides* and *M. mansuyi* were found only in Lake Dianchi (in August 2008) and Lake Xingyun (in November 2007), respectively (Fig. 1). Juveniles of *M. mansuyi* were collected as free crawling hatchlings in the same samples as the adults. Voucher specimens have been deposited with the Institute of Hydrobiology (IHB), Chinese Academy of Sciences (CAS), Wuhan, China.

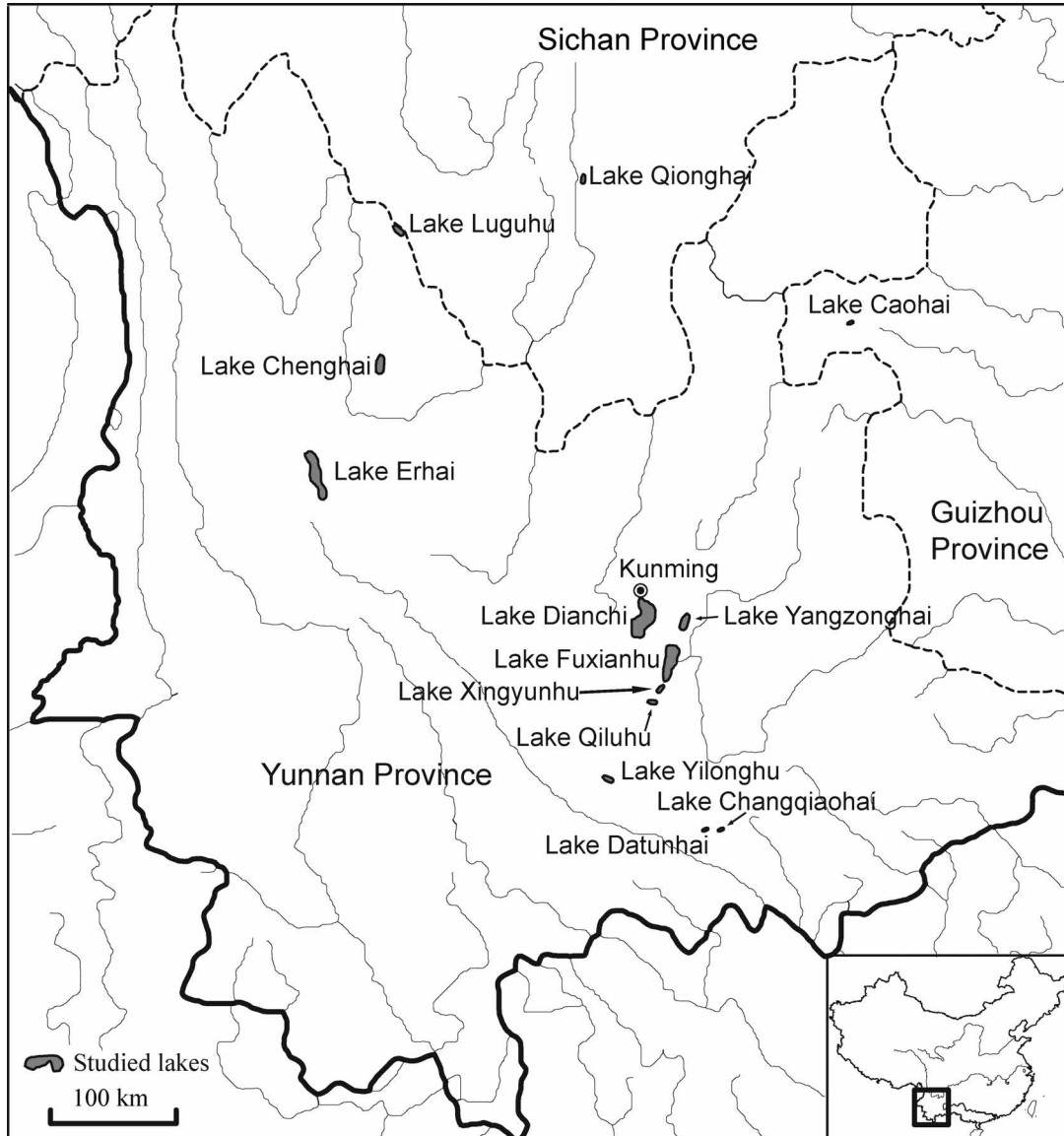


FIGURE 1. Map of sampling sites in Yunnan Province, southwest China.

TABLE 1. Surface area, depth, altitude and lakes sampled on Yunnan-Guizhou Plateau.

	Surface area (km ²)	Maximum depth (m)	Mean depth (m)	Altitude (m)	Sampling sites	
					Number	Water depth (m)
Lake Dianchi	297.9	7	2.9	1886	30	1.9–6.8
Lake Xingyun	35	11	7.8	1722	14	5.2–10.6
Lake Fuxian	211	155	90	1721	42	1.9–140
Lake Yangzonghai	32	30	19.5	1770	12	2–27.7
Lake Qilu	36.9	6.8	4.0	1796	20	1.2–6.3
Lake Erhai	249	20.7	10.2	1973	20	1.6–20.3
Lake Yilong	38	6.2	2.4	1412	8	1.2–5.6
Lake Chenghai	77	35.1	25.7	1503	8	1.1–32.1
Lake Lugu	56	93.5	40.5	2690	10	1.5–68.7
Lake Datun	12.3	5	3.7	2171	4	3.3–4
Lake Changqiao	10.7	5.5	3.7	1284	5	1.3–4.1
Lake Qionghai	31	34	10.3	1509	5	1.5–17.8
Lake Caohai	25	5	2.4	1286	6	1.1–2.4

Dimensions of adult and juvenile shells were measured with vernier callipers (precision 0.1 mm). Radulae were extracted from the buccal mass by soaking in 2% sodium hydroxide solution for 24 h at room temperature. Each radula was then rinsed with distilled water until all remaining tissue was removed. The radulae were mounted individually on copper stubs. After air-drying, they were coated and examined with a FEI QUANTA 200 scanning electron microscope.

Systematic descriptions

Viviparidae Gray, 1847

The viviparid fauna of China is highly diverse with nine genera and about 70 species (Yen 1939; Liu *et al.* 1995), which comprise about 50% of the world's viviparid fauna (Strong *et al.* 2008). Two genera (*Margarya* Nevill, 1877 and *Rivularia* Heude, 1890) and at least 80% of all viviparid species are endemic to China.

Margarya Nevill, 1877

Margarya Nevill, 1877: 30–31. Type species: *Margarya melanioides* Nevill, 1877, by subsequent designation in Yen (1939: 41; 1943: 128) and Tchang and Tsi (1949: 5).

Diagnosis

Shell large, up to about 70 mm in width, thick and extremely stout; 6–7 shouldered whorls, a very clear ramp-like area on the upper portion of each whorl, generally with prominent keels, tubercles or spines; apex obtuse; aperture ovate; umbilicus small or absent; operculum corneous and ovate.

Margarya melanioides Nevill, 1877

Margarya melanioides Nevill, 1877: 30–31 (Lake Er-Hai, Yunnan Province); Yen 1939: 41, pl. 2, fig. 60; Yen 1943: 128; Tchang and Tsi 1949: 5–8, fig. 1–4; Xia 1982: 340–341, fig. 9; Liu *et al.* 1995: 14; Liu and Wu 2005: 299–300.

Vivipara delavayi Mabilie, 1886: 66, pl. II, figs 1a, 1b.

Material examined

Lake Dianchi, Yunnan Province, Southwest China (21 voucher specimens IHB YAN 20080801, 24°47'56.0" N, 102°44'09.6" E).

Morphology

Shell (Fig. 2A–E, Table 2): Large, average height 51 mm, average width 35 mm; greenish or yellowish brown, thick, stout, with turreted spire. Seven convex whorls, shouldered; deep suture; apex blunt. Last whorl greatly inflated, comprising around 40% of shell height; with 6–9 (mostly 9) spiral keels of variable development, spire whorls with three spiral keels. Development of spiral keels on last whorl varies greatly; second keel usually conspicuously elevated, first and third keels moderately developed, all other keels decrease in strength gradually towards base of shell. Second keel may support row of large, triangular spines on last whorl and penultimate whorl; small nodules may form on second and third spiral whorl; all other keels smooth. Aperture ovate, slightly more than half of shell height, flattened above, with obtuse angle. Inner lip slightly thickened, reflected. Umbilicus completely covered by inner lip.

Operculum: Brown or yellowish brown, thin, corneous, ovate, with sub-central nucleus and concentric growth lines (Fig. 2F).

Mantle cavity: Mantle edge smooth. Monopectinate ctenidium with large, elongate triangular filaments, extending from base of pallial cavity to mantle margin.

Osphradium pale yellow, forming an elongate, narrow ridge on pallial roof, approximately as long as ctenidium.

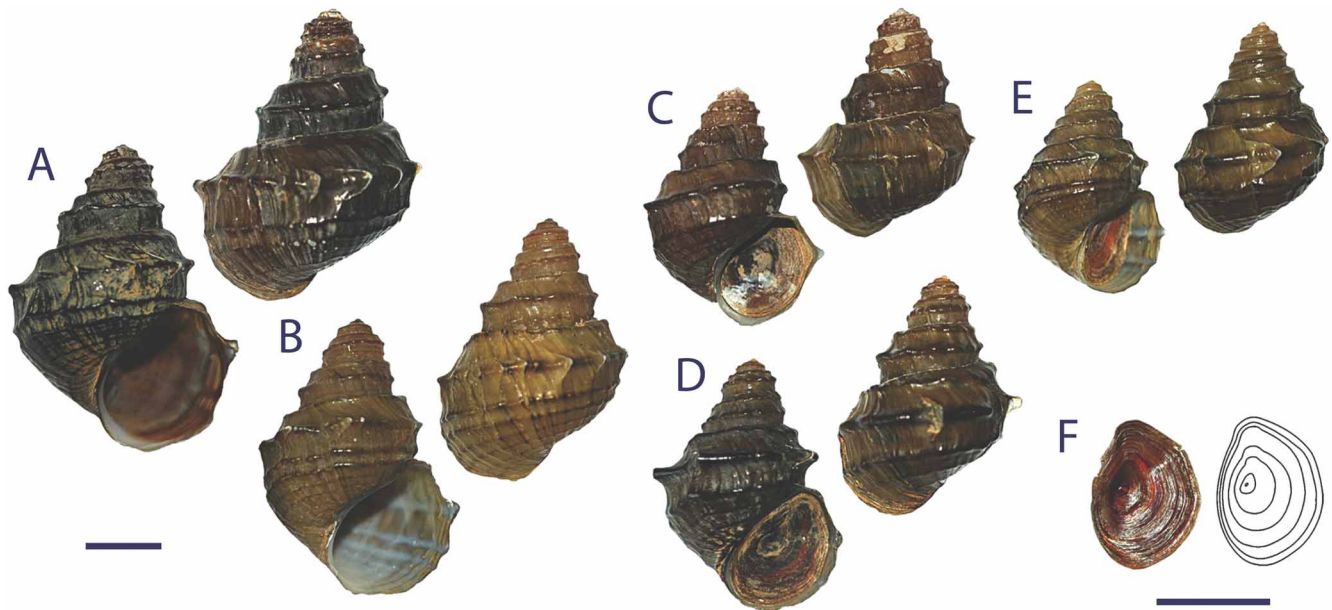


FIGURE 2. Shells and operculum of *Margarya melanioides* from Lake Dianchi (IHB YAN 20080801). A–E, shells, F, operculum. Scale bars = 10 mm.

TABLE 2. Shell parameters (mean \pm standard deviation/size range) of *Margarya melanioides* and *Margarya mansuyi*.

	<i>M. melanioides</i>	<i>M. mansuyi</i>
Shell height (mm)	50.6 \pm 4.237/43.73–58.58	28.1 \pm 15.300/10.19–50.43
Shell width (mm)	35.5 \pm 3.402/29.62–41.67	16.8 \pm 7.705/7.99–29.54
Aperture height (mm)	36.0 \pm 3.077/30.61–41.99	13.5 \pm 6.156/5.84–21.97
Aperture width (mm)	25.9 \pm 2.470/21.22–29.87	10.3 \pm 4.591/4.56–16.51
Body whorl height (mm)	19.9 \pm 1.925/16.88–24.26	19.2 \pm 8.508/9.01–31.79
Shell height/shell width	1.43 \pm 0.083/1.22–1.57	1.59 \pm 0.224/1.24–2.01
Shell height/body whorl height	2.55 \pm 0.111/2.38–2.84	1.39 \pm 0.199/1.05–1.71
Aperture width/aperture height	0.77 \pm 0.027/0.72–0.81	0.77 \pm 0.028/0.72–0.82
Aperture height/shell height	0.51 \pm 0.028/0.45–0.56	0.51 \pm 0.0073/0.41–0.67
Number of whorls	7	4–7
Number of specimens	21	20

Radula (Fig. 3A–C): Ribbon oblong, length 6.0–6.3 mm, width 0.7–0.9 mm, consisting of 108–128 rows of teeth ($n = 3$). Central tooth bell-shaped, central cusp large, broad, squarish; flanked by 5–6 smaller, pointed denticles on each side that taper in size. Lateral teeth broadly oblong, with one large, square central denticle and 4–5 smaller cusps on each side. Marginal teeth slender, slightly oblong. Inner marginal teeth possess one large central denticle and 3–4 smaller cusps on each side. Outer marginal teeth obtuse at tip, with 11–13 smaller cusps on two thirds of inner part of front edge.

Distribution

In the current survey found only in Lake Dianchi, Yunnan Province, Southwest China. According to Tchang

and Tsi (1949) and Zhang *et al.* (1997), it was widely distributed in lakes of Yunnan, such as Lakes Dianchi, Er-Hai, Fuxian, I-lung and Ta-tun-hai.

Remarks

This species was described for its '*Melania*'-like spire and distinct spiral keels. Most species-group taxa of *Margarya* have historically been considered as forming subspecies or varieties of *M. melanioides* (e.g., Dautzenberg and Fischer 1905; Yen 1939, 1943). Dautzenberg and Fischer (1905) also referred to the variety name '*Vivipara margeriana*', which was originally attributed to Nevill by Neumayr (1883: 24). However, we were unable to trace a description of this taxon by Nevill and therefore regard this

name as a *nomen nudum* introduced by Neumayr (1883). As many other nominal species-group taxa, *Vivipara delavayi* Mabilie, 1886 was treated by Dautzenberg and Fischer (1905) as a variety of *M. melanioides* and as a junior synonym of the latter by Yen (1943) and Tchang and Tsi (1949). *M. melanioides* can be distinguished from other congeners by its relatively large size, inflated whorls, the larger number of spiral keels and large, triangular spines on the last two whorls. The species is highly variable and shows polymorphic shell characters in the same population,

particularly with regard to the development of the spiral keels (Tchang and Tsi 1949). Four shell types were discriminated by Zhang (1986), of which their type A has been the one most commonly found (Zhang 1986). Most specimens (>80% of 21 specimens) from our recent collection belong to type A, in which large, triangular spines exist on the last two whorls. Radulae as shown here differ from the illustrated specimens of Tchang and Tsi (1949) and Zhang (1986) in details of the tooth shape and number of cusps. No juveniles were found in this study.

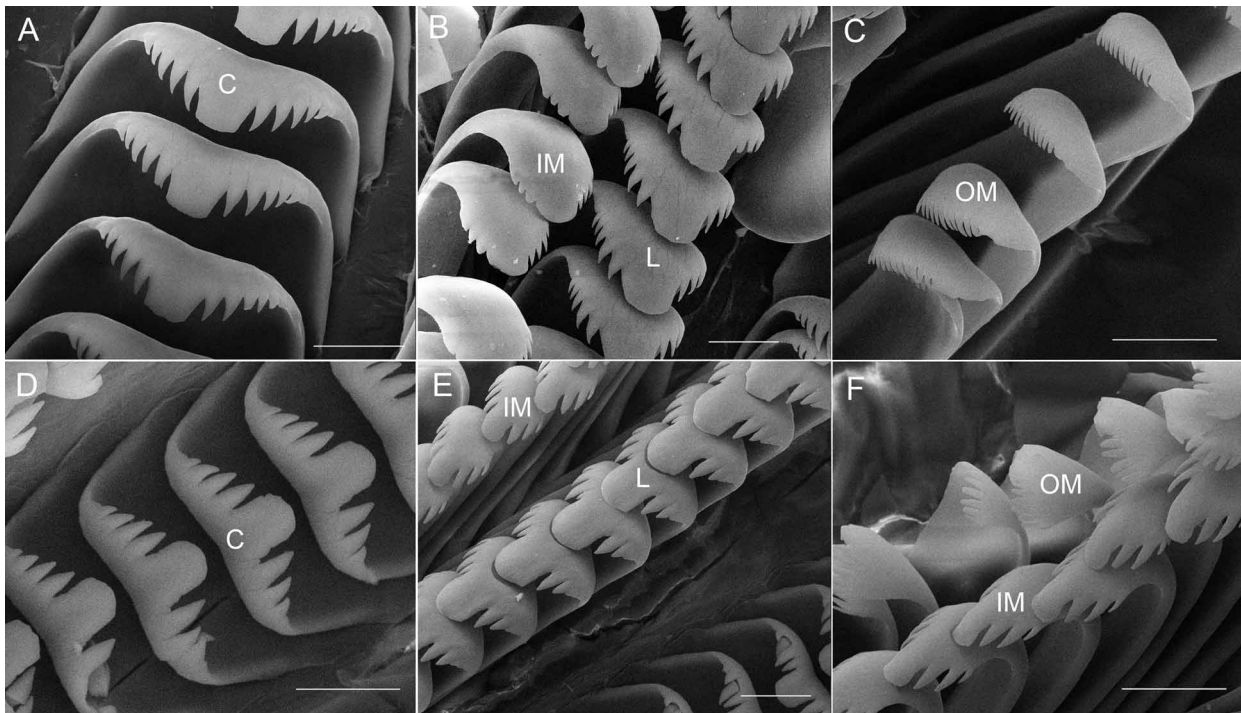


FIGURE 3. Radulae. A–C, *Margarya melanioides* (IHB YAN 20080801), D–F, *Margarya mansuyi*, (IHB YAN 20071102). Abbreviations: C—central tooth, L—lateral tooth, IM—inner marginal tooth, OM—outer marginal tooth. Scale bar = 50 μ m.

Margarya mansuyi Dautzenberg & Fischer, 1905

Margarya melanioides var. *mansuyi* Dautzenberg & Fischer, 1905: 423–424, figs 2–4. (Mongtze, Yunnan Province).

Margarya melanioides mansuyi - Yen 1939: 41, pl. 2, fig. 61; Yen 1943: 128.

Margarya mansuyi - Tchang and Tsi 1949: 5–8, fig. 1–4; Liu *et al.* 1995: 14; Liu and Wu 2005: 302–303.

Material examined

Lake Xingyun, Yunnan Province, Southwest China (20 voucher specimens IHB YAN 20071102, 24°21'18.8" N, 102°47'22.0" E).

Morphology

Shell (Fig. 4A–D, Table 2): Large, in average 41 mm high, 23 mm wide; yellowish brown, slightly transparent, thick, stout, conical. Seven whorls, nearly cylindrical, shouldered, with deep suture; apex blunt. Spire comprising about 63% of height of shell, not elevated; last whorl slightly inflated, with 3–4 spiral keels of variable development; subsequent whorls typically with 3, rarely 2, spiral keels.

Spiral keels conspicuously elevated, always smooth. Aperture ovate, less than half of shell height, with obtuse angle above. Lip thick, solid. Inner lip reflected, partly concealing umbilicus. Umbilicus small, narrowly open.

Juvenile shell (Fig. 4E, F): Broadly conical, brown, moderately transparent. With 5–6 whorls, typically 4 well developed spiral keels on last whorl, of which second keel is reduced. On subsequent whorls, second and fourth keel obscured. Aperture ovate, clearly more than half of shell height.

Dimensions: See Table 2. Two size cohorts (or age cohorts) can be clearly separated within population of *M. mansuyi* (Fig. 5), which represent adults (30–50 cm in shell height) and juveniles (10–15 cm in shell height), respectively. The H/W ratio of juveniles is identical with that of adults.

Operculum: Dark brown in color, corneous, ovate in shape, with sub-central nucleus and concentric growth lines (Fig. 4G).

Mantle cavity organs: Identical with *M. melanioides*.

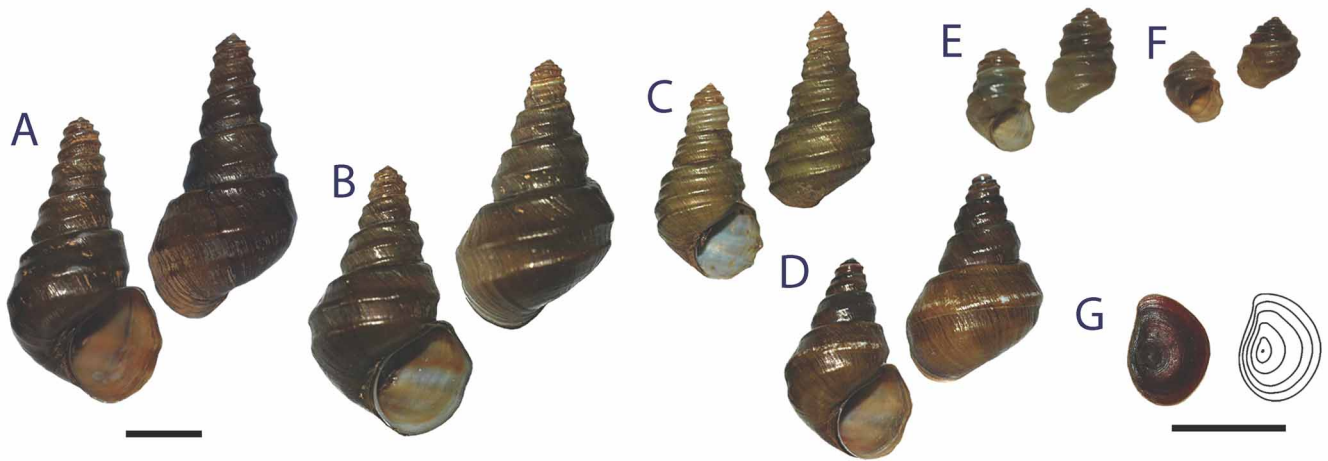


FIGURE 4. Shells and operculum of *Margarya mansuyi* from Lake Xingyun (IHB YAN 20071102). **A-D**, adult shells, **E-F**, juvenile shells, **G**, operculum. Scale bars = 10 mm.

Radula (Fig. 3D–F): Ribbon oblong, length 4.8–5.5 mm, width 0.6–0.7 mm, with about 105–110 rows of teeth ($n = 3$). Central tooth trapezoid, symmetrical, with 9–10 cusps; central cusp large, squarish, flanked by 4–5 smaller denticles on each side. Lateral tooth broadly oblong, with slightly enlarged central denticle and 3–5 small cusps on each side of it. Marginal tooth, slender, slightly oblong. Inner marginal tooth with large, ligulate central cusp and 3–4 smaller cusps on each side of it. Outer marginal tooth obtuse, with 5–9 small cusps.

Distribution

Endemic to Lake Xingyun and, according to Tchang and Tsi (1949), Lake Ta-tun-hai, Yunnan Province, Southwest China.

Remarks

This taxon was described as a variety of *Margarya melanioides* and subsequently raised to subspecies-level by Yen (1939) and then treated as a distinct species by Tchang and Tsi (1949), Liu *et al.* (1995) and Liu and Wu (2005). *Margarya mansuyi* and *M. melanioides* can be discriminated e.g., by morphometric shell parameters such as the ratios height/width of shell (H/B) or height of shell/ height of last whorl (H/BW) (Figs 5–6). Note that juveniles and adults of *M. mansuyi* form two separate clusters in Figure 5 with corresponding allometry. The two species also differ greatly in the number and development of the spiral keels and in the number of cusps on outer marginal tooth. *M. mansuyi* resembles *M. bicostata* in shell shape, but the latter has only three keels on the last whorl and two spiral keels on subsequent whorls.

Discussion

Traditionally, shell characters have been emphasized in taxonomic treaties. Indeed, the shell bears many characters convenient for taxonomic purposes, which are accessible also from dry material and fossils (e.g., Smith 1981;

Ridgeway *et al.* 1998). On the other hand, the shell may be prone to environmental pressures, and cases of phenotypic plasticity in shell morphology have been reported from various gastropod groups (e.g., Vermeij and Covich 1978; Reid 1986, 1992; Reed and Janzen 1999; Warner 1996; Urabe 1998). Hence, before shell features are used for taxonomic purposes, the extent of infraspecific variation must be assessed. In the present case plotting morphometric size ratios, such as height/width or height of last whorl/ height of shell against each other has been sufficient to demonstrate that the two taxa occupy distinct morphospaces.

The radula has been an important source of information from the early days of gastropod systematics (e.g., Trochel 1856-63; Thiele 1929). In Viviparidae the radula is conservative, showing little interspecific differences with respect to the pattern of dentition (e.g., Falniowski *et al.* 1996). Correspondingly, we found little differentiation between the two congeneric species studied here and conclude that in this case the radula is of limited value in the delineation of these species.

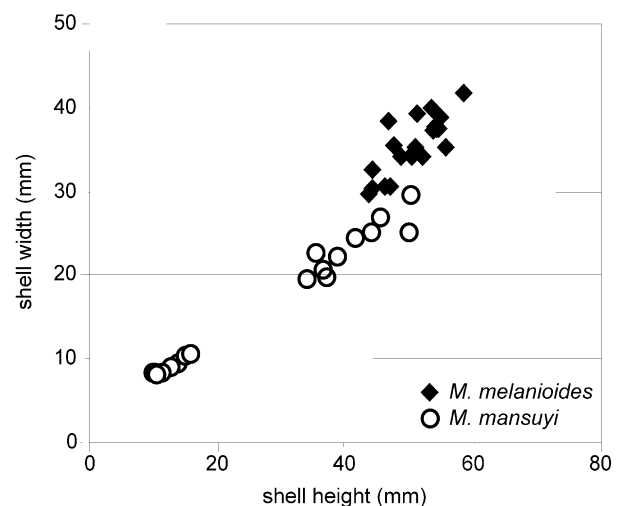


FIGURE 5. Scatter plot showing comparison of *Margarya melanioides* and *Margarya mansuyi* with respect to shell height and width (mm).

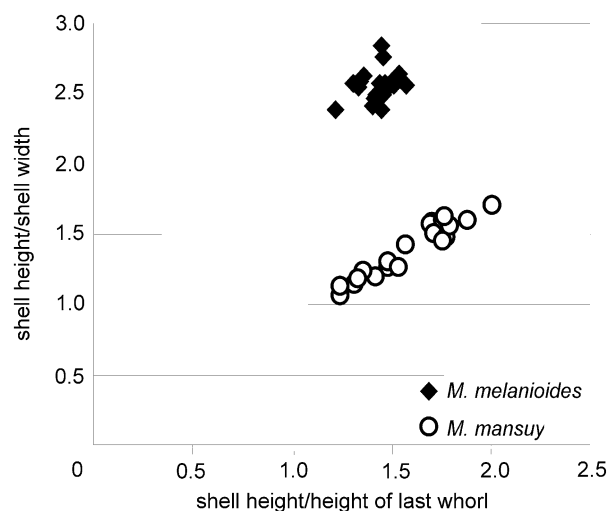


FIGURE 6. Scatter plot showing comparison of *Margarya melanioides* and *Margarya mansuyi* with respect to the parameters shell height/body whorl height and shell height/shell width.

The Yunnan-Guizhou Plateau in southwest China, Yunnan Province, comprises a multitude of tectonic lakes with a complex geological history. These lakes are known to harbour a unique fauna of fish and oligochaetes (Li *et al.* 1963; Gao *et al.* 1989; Cui *et al.* 2008), as well as at least 124 gastropod species, most of which are endemic (Zhang *et al.* 1997). Freshwater molluscs have become increasingly threatened world-wide due to the pollution or eutrophication of water bodies, the destruction of habitats, or introduction of invasive species (Lydeard *et al.* 2004; Strong *et al.* 2008). In Yunnan, the ecological degradation of the lakes due to pollution and overharvesting has resulted in a dramatic decline of numerous freshwater molluscs. Among them species of *Margarya* are likely to represent the most endangered group. All eleven currently recognized species were listed in the Red List of China; two species are considered vulnerable, four endangered, one extremely endangered, and four extinct (Liu and Wu 2005). Some decades ago, in the 1940s–1960s, *Margarya* species were the predominant molluscan taxa in those lakes (Tchang and Tsi 1949; Zhang 1986). For Lake Dianchi, Tchang and Tsi (1949) reported on densities of 36 individuals/m², which is the only available quantitative data. In contrast to these historical reports, in our survey just a few specimens of *Margarya* species were found in only two lakes. We spent about four hours with a triangular dredge collecting the 21 specimens of *M. melanioides* and no living individuals were found in any of the quantitative samples. It is difficult to compare our sampling methods and efforts with those of earlier surveys due to the unavailability of detailed records, although most earlier sampling was qualitative. Even though a statistically valid analysis of sampling is not possible, it is very clear that *Margarya* in the lakes of the Yunnan Plateau has faced a massive decline in recent decades and may have become entirely or nearly extinct in many of them. This finding underscores the notion that the decline of freshwater gastropods is a general phenomenon observed worldwide with particular relevance at regional and local scales (Neves

et al. 1997, Ponder & Walker 2003; Lydeard *et al.* 2004; Strong *et al.* 2008). As holds true for many other gastropods in China, detailed and actual information on the biology and current distribution of *Margarya* is scarce. Further studies of the biology of these species are urgently needed in order to provide vital information to assist conservation efforts.

Acknowledgements

This study is part of the project ‘Surveys on biological resources of lakes on the Yunnan-Guizhou Plateau’ (No. 2006FYII0600). We thank Dr. Yongde Cui and Dr. Xueqin Liu for their help in the field survey and Winston Ponder (Sydney) and Hiroshi Fukuda (Okayama) for their helpful reviews.

References

- Chen, Y.X., Zhang, N.G., Zhang, W. & Li, J.K. (1996) The karyotype study of *Margarya yaungtsunghaiensis* and *M. melanioides* (Viviparidae). *Zoological Research* 17, 94–96. (In Chinese with English abstract)
- Cui, Y.D., Liu, X.Q. & Wang, H.Z. (2008) Macrozoobenthic community of Fuxian Lake, the deepest lake of southwest China. *Limnologia* 38, 116–125.
- Dautzenberg, P. & Fischer, H. (1905) Liste de mollusques récoltés par M. Mansuy en Indo-Chine et description d'espèces nouvelles. *Journal de Conchyliologie* 53, 343–471.
- Falniowski, A., Mazan, K. & Szarowska, M. (1996) Tracing the viviparid evolution: radular characters (Gastropoda: Architaenioglossa: Viviparidae). *Malakologische Abhandlungen, Staatliches Museum für Tierkunde Dresden* 18, 43–52.
- Gao, L.C., Zhuang, D.D. & Wang, Y.H. (1989) *Fishery resources of lakes in Yunnan Plateau*. Jiangsu Science and Technology Press, Nanjing. (In Chinese)
- Li, S.H., Yu, M.J., Li, G.Z., Zeng, J.J., Chen, J.Y., Gao, B.Y. & Huang, H.J. (1963) Investigations on lakes in Yunnan Plateau. *Oceanologia et Limnologia Sinica* 5, 87–112. (In Chinese with English abstract)
- Liu, Y.Y. & Wu, M. (2005) Mollusca. In: Wang, S. & Xie, Y. (Eds.), *China Species Red List. III. Invertebrates*. Higher Education Press, Beijing, pp. 299–306. (In Chinese)
- Liu, Y.Y., Zhang, W.Z. & Wang, Y.X. (1995) Distribution of the family Viviparidae from China (Mollusca: Gastropoda). *Transactions of the Chinese Society of Malacology* 5–6, 9–17. (In Chinese with English abstract)
- 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., Hershler, R., Perez, K.E., Roth, B., Seddon, M., Strong, E.E. & Thompson, F.G. (2004) The global decline of nonmarine mollusks. *BioScience* 54, 321–330.
- Mabille, J. (1886) Description de vivipares nouvelles du Lac Ta-Ti. *Bulletin de la Société de France* 3, 65–76.
- Neumayr, M. (1883) Über einige Süßwasserconchylien aus China. *Neues Jahrbuch für Mineralogie* 1883(2), 21–26.
- Neves, R.J., Bogan, A.E., Williams, J.D., Ahlstedt, S.A. & Hartfield, P.W. (1997) Status of aquatic mollusks in the southeastern United States: a downward spiral of diversity. In: G. W. Benz and D. E. Collins, (eds.) *Aquatic Fauna in Peril*. Southeast Aquatic Research Institute Special Publication 1, Lenz Design and Communications, Decatur, Georgia. 43–85.
- Nevill, G. (1877) List of the Mollusca brought back by Dr. Anderso

- n from Yunan and Upper Burma, with descriptions of new species. *Journal of the Asiatic Society of Bengal* 96, 14–41.
- Ponder, W.F. & Walker, K.F. (2003) From mound springs to mighty rivers: the conservation status of freshwater molluscs in Australia. *Aquatic Ecosystem Health & Management* 6, 19–28.
- Reed, W.L. & Janzen, F.J. (1999) Natural selection by avian predators on size and colour of a freshwater snail (*Pomacea flagellata*). *Biological Journal of the Linnean Society* 67, 331–342.
- Reid, D.G. (1986) *The littorinid molluscs of mangrove forests in the Indo-Pacific region. The genus Littoraria*. British Museum (Natural History), London.
- Reid, D.G. (1992) Predation by crabs on *Littoraria* species (Littorinidae) in a Queensland mangrove forest. *Proceedings of the Third International Symposium on Littorinid Biology*, 141–151.
- Ridgeway, T.M., Stewart, B.A., Branch, G.M. & Hodgson, A.N. (1998) Morphological and genetic differentiation of *Patella granularis* (Gastropoda: Patellidae): recognition of two sibling species along the coast of southern Africa. *Journal of Zoology* 245, 317–313.
- Smith, J.E. (1981) The natural history and taxonomy of shell variation in the periwinkles *Littorina saxatilis* and *Littorina rudis*. *Journal of the Marine Biological Association of the United Kingdom* 61, 215–241.
- Strong, E.E., Gargominy, O., Ponder, W.F. & Bouchet, P. (2008) Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia*, 595, 149–166.
- Tchang, X. & Tsi, Z.Y. (1949) A revision of the genus *Margarya* of the family Viviparidae. *Contributions from the Institute of Zoology National Academy of Peiping* 5, 1–26.
- Thiele, J. (1929) *Teil 1. Loricata; Gastropoda: Prosobranchia. Handbuch der Systematischen Weichtierkunde*. Gustav Fischer, Jena.
- Troschel, F.H. (1856–1863) *Das Gebiss der Schnecken zur Begründung einer natürlichen Classification*, 1. Nicolaische Verlagsbuchhandlung, Berlin.
- Urabe, M. (1998) Contribution of genetic and environmental factors to shell shape and variation in the lotic snail *Semisulcospira reiniana* (Prosobranchia: Pleuroceridae). *Journal of Molluscan Studies* 64, 329–343.
- Vermeij, G.J. & Covich, A.P. (1978) Coevolution of freshwater gastropods and their predators. *American Naturalist* 112, 833–843.
- Warner, G.F. (1996) Factors affecting the selection of pond snail prey by signal crayfish. *Freshwater Crayfish* 11, 194–202.
- Xia, W.P. (1982) The subfossil *Margarya* (Gastropoda, Viviparidae) from west coast of Kunming Lake, with a discussion of its evolution. *Zoological Research* 3, 339–348.
- Yen, T.C. (1939) Die chinesischen Land- und Süßwasser-Gastropoden des Natur-Museums Senckenberg. *Abhandlungen der senckenbergisch-naturforschenden Gesellschaft* 444, 1–233.
- Yen T.C. (1943) A preliminary revision of the Recent species of Chinese Viviparidae. *Nautilus* 56, 124–130.
- Zhang, L. (1986) Study on the morphological variation of *Margarya melanioides* and *M. monodi* from Dian-Chi, Yunnan. *Transactions of the Chinese Society of Malacology* 2, 65–71. (In Chinese with English abstract)
- Zhang, N.G., Hao, T.X., Wu, C.Y., Chen, Y.X., Zhang, W., Li, J.F. & Zhang, Y. (1997) Primary investigation of freshwater Gastropoda in Yunnan Province. *Studia Marina Sinica* 39, 15–26. (In Chinese with English abstract)