

Morphological analysis of the Chinese *Cipangopaludina* species (Gastropoda; Caenogastropoda: Viviparidae)

Hong-Fa LU^{1,†}, Li-Na DU^{2,†}, Zhi-Qiang LI^{1,*}, Xiao-Yong CHEN^{3,*}, Jun-Xing YANG^{3,*}

1. Zhejiang Normal University, Xiaoshan Campus, Hangzhou 311231, China

2. Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming 650223, China

3. State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming 650223, China

Abstract: Viviparidae are widely distributed around the globe, but there are considerable gaps in the taxonomic record. To date, 18 species of the viviparid genus *Cipangopaludina* have been recorded in China, but there is substantial disagreement on the validity of this taxonomy. In this study, we described the shell and internal traits of these species to better discuss the validity of related species. We found that *C. ampulliformis* is synonym of *C. lecythis*, and *C. wingatei* is synonym of *C. chinensis*, while *C. ampullacea* and *C. fluminalis* are subspecies of *C. lecythis* and *C. chinensis*, respectively. *C. dianchiensis* should be placed in the genus *Margarya*, while *C. menglaensis* and *C. yunnanensis* belong to genus *Mekongia*. Totally, this leaves 11 species and 2 subspecies recorded in China. Based on whether these specimens' spiral whorl depth was longer than aperture depth, these species or subspecies can be further divided into two groups, viz. *chinensis* group and *cathayensis* group, which can be determined from one another via the ratio of spiral depth and aperture depth, vas deferens and number of secondary branches of vas deferens. Additionally, Principal Component Analysis indicated that body whorl depth, shell width, aperture width and aperture length were main variables during species of *Cipangopaludina*. A key to all valid Chinese *Cipangopaludina* species were given.

Keywords: *Cipangopaludina*; Gastropoda; Bellamyinae; Anatomy; Taxonomy; Chinese

The freshwater gastropod Viviparidae is currently divided into three subfamilies (Bouchet & Rocroi, 2005): Viviparinae Gray, 1847, Bellamyinae Rohrbach, 1837 and Lioplacinae Gill, 1863, which together comprise approximately 150 species and 31 genera recognized to date (Franke et al, 2007). Typically, viviparid species inhabit lakes, ponds, and lentic rivers of temperate to tropical region (Strong et al, 2008; Ying et al, 2013), explaining their wide global distribution across every continent save for South America and Antarctica (Brown, 1994). In China, the existing taxonomy for Viviparidae includes approximately 61 recognized species in 9 genera (Du et al, 2011; Liu, 1991; Wang & Xie, 2005; Yen, 1943): *Viviparus* Montfort, 1810, *Bellamyia* Jousseaume, 1886, *Filopaudina* Habe, 1964, *Mekongia* Crosse et Fischer, 1876, *Angulyagra* Benson, 1836, *Margarya* Nevill, 1877, *Rivularia* Heude, 1890 and *Trochotaia* Brandt, 1974, *Cipangopaludina* Hannibal, 1912. The last genus, *Cipangopaludina* is particularly interesting as a

diverse genus mainly distributed in China, Japan, Korea, Thailand, Vietnam, Laos, India, Burma and Malaya (Brandt, 1974; Liu et al, 1993) that is comprising of 35 species and subspecies (Global Names Index; <http://gni.Globalnames.org>), there has been substantial debate on the taxonomy of *Cipangopaludina*. Hannibal (1912) had previously proposed *Cipangopaludina* as a subgenus of *Idiopoma*, based on invasive specimens collected in California which were identified as *Paludina malleata*

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*Corresponding authors, E-mail: hxlzq@zjou.edu.cn; chenxy@mail.kiz.ac.cn; yangjx@mail.kiz.ac.cn

†Authors contributed equally to this work

Reeve. Meanwhile, Annandale (1920) proposed *Lecythoconcha* as a distinct genus for *Paludina lecythis* Benson while Prashad (1928) argued that *Lecythoconcha* was invalid and adopted the name *Cipangopaludina*.

Even within China, there is no clear verdict on the validity of each species or how many are even distributed in the area. Heude (1890) listed 9 species from China, viz. *C. chinensis* (Benson (non Gray)), *C. lecythoides* (Heude), *C. diminuta* (Heude), *C. longispira* (Heude), *C. fluminalis* (Heude), *C. leucostoma* (Heude), *C. cathayensis* (Heude), *C. ventricosa* (Heude) and *C. aubryana* (Heude). Later, comprehensive work by Kobelt (1909) revised Viviparidae, including practically all the forms of the family known at the time, which was one species and 12 subspecies in China, with most of species being designated varieties of the species *C. chinensis* (Gray): *cathayensis* (Heude), *compacta* (Nevill), *ventricosa* (Heude), *longispira* (Heude), *fluminalis* (Heude), *hainanensis* (Kobelt), *diminuta* (Heude), *leucostoma* (Heude), *aubryana* (Heude), *patris* (Kobelt), *wingatei* (Smith), *lecythoides* (Benson) and its form *latissima* (Dautzenberg et H. Fischer). Several decades later, Yen (1943) revised species of Chinese Viviparidae, and pointed out that *leucostoma* and *diminuta* were synonyms of *chinensis* and that *lecythoides* (Heude, non Benson) distributed in Zhoushan Island, *compacta* (Kobelt, non Nevill) distributed in Hainan, and *lecythis crassior* (Annandale) distributed in western Yunnan were all synonyms of *patris* (Kobelt), and *longispira* (Heude) was argued to be synonymous with *haasi*. Liu (1991) later clarified the distribution and taxonomy of *Cipangopaludina* and raised 15 of the subspecies to the species level, viz. *C. chinensis*, *C. cathayensis*, *C. fluminalis*, *C. aubryana*, *C. latissima*, *C. lecythoides*, *C. ussuriensis* (Gerstfeldt), *C. yunnanensis*, *C. dianchiensis*, *C. ampullacea*, *C. haasi*, *C. lecythis*, *C. longispira*, *C. ventricosa* and *C. menglaensis*. Finally, Wang & Xie (2005) evaluated the extinction risk of *Cipangopaludina* species, listing 14 distinct species: *Cipangopaludina hainanensis*, *C. leucostoma*, *C. menglaensis*, *C. latissima*, *C. dianchiensis*, *C. lecythis*, *C. lecythoides*, *C. haasi*, *C. ampullacea*, *C. ventricosa*, *C. ampulliformis*, *C. aubryana*, *C. longispira* and *C. ussuriensis*. Curiously, these latest works by Liu (1991) and Wang & Xie (2005) made no mention of two species, *C. patris* and *C. wingatei*, and ignored some of the earlier work done by Yen (1943).

Despite discrepancies and arguments as well as the

elevation and demotion of species to subspecies and vice versa, the existing literature names 18 potential species of *Cipangopaludina* distributed in China: *C. ampullacea*, *C. ampulliformis*, *C. aubryana*, *C. cathayensis*, *C. chinensis* (synopsis *C. leucostoma* and *C. diminuta*), *C. dianchiensis*, *C. fluminalis*, *C. haasi* (synopsis *C. longispira*), *C. hainanensis* (synopsis *C. compacta*), *C. latissima*, *C. lecythoides*, *C. lecythis*, *C. menglaensis*, *C. patris*, *C. ussuriensis*, *C. ventricosa*, *C. wingatei* and *C. yunnanensis*. Similarly, the disparate results of the previous studies on the topic also highlight how difficult and complex the identification of *Cipangopaludina* is, largely due to intraspecific variations in shell shape. This has left the taxonomic position and phylogenetic relationships of these species largely unknown. In this study, we opted to perform a fresh check on the morphology and anatomy of Chinese *Cipangopaludina* species currently being held at repositories in Beijing and Kunming in order to arrive at a more complete species list. Morphometric analyses of shell variations were conducted on *Cipangopaludina* species through a Principal Component Analysis.

MATERIALS AND METHODS

Sample collection and identification

Four hundred and ninety-six, including 11 *Cipangopaludina* species were collected from Jilin, Jiangxi, Zhejiang, Guangxi and Yunnan Provinces. These specimens were preserved in Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ). Additionally, 145 *Cipangopaludina* specimens, including 18 *Cipangopaludina* species or its synonyms listed in the existing literature preserved in the Invertebrate Museum of the Institute of Zoology, Chinese Academy of Sciences, Beijing (IOZ) were measured. A morphological analysis was conducted on these specimens and the validity of the currently identified species was determined. Specimens were identified mainly based on original description, type specimens, Liu et al (1979, 1993), Kobelt (1909) and Prashad (1928).

Characters selected for morphometric analysis

To select characters for use in morphometric analysis, we reviewed the available taxonomic descriptions from literature (Liu et al, 1979). Five shell characters were measured with callipers accurate to 0.1 mm: Shell depth (D), the maximum dimension parallel to the axis of coiling; Shell width (W) the maximum dimension

perpendicular to D; Length of the aperture (LA), the maximum dimension from the junction of the outer lip with the penultimate whorl to the anterior edge of the aperture (oblique to coiling axis); width of the aperture (WA), the maximum dimension perpendicular to LA; depth of the body whorl (BW), the dimension from the lower margin of the aperture to the upper suture delimiting the first whorl; and N, the number of whorls.

Embryonic shells were measured to 0.1 mm using an ocular micrometer. Anatomy was studied using a microscope with drawing apparatus. Radulae and embryonic shells were studied via scanning electron microscopy (SEM). The radulae were cleaned enzymatically with proteinase K, as described by Holznagel (1998), then sonicated and mounted on aluminium specimen stubs with adhesive pads. Embryonic shells were cleaned mechanically, sonicated, and mounted on adhesive carbon-coated pads. Both radulae and embryonic shells were coated with gold-palladium and studied on AMRAY 1000B scanning electron microscope at 30 kV. The description of shell features and visceral hump follows the general terminology suggested by Simone (2004).

Allometric shell growth

Due to ontogenetic effect of allometric growth have usually caused confusion in morphometric analyses, these individuals within the range of allometric growth were eventually excluded before multivariate analyses (Armbruster, 1995; Chiu *et al.*, 2002; Valovirta & Vaisanen, 1986). However, in the present-day study, it is difficult for us to obtain snails of all size classes from each population per species and examine the allometric shell growth. Under this circumstance, the consequence of Chiu *et al.* (2002) was followed that excluded individuals with aperture lengths of less than 1.0 cm. Morphometric data was explored through a Principal Component Analysis by SPSS 10.0 (SPSS for Windows, Chicago, IL, USA).

RESULTS

Systematics *Cipangopaludina* Hannibal, 1912

Idiopoma (*Cipangopaludina*) Hannibal 1912, *Proceedings of the Malacological Society of London* 10: 194 (type species, *Paludina malleata* Reeve, original designation)

Lecythoconcha Annandale 1920, *Records of the Indian Museum*. 19: 111 (type species, *Paludina lecythis* Benson, monotypic); Annandale 1921, *Records of the*

Indian Museum, 6: 401.

Viviparus (*Cipangopaludina*), Clench & Fuller, 1965, *Occasional papers on Mollusks, Museum of Comparative Zoology*, 2: 385–412.

Bellamyia (*Cipangopaludina*), Smith, 2000, *Nautilus*, 114(2): 31–37.

Diagnosis: Shell medium to large (up to 70 mm), oval, brown or greenish in colour. Apex pointed or obtused. Suture narrow. Umbilicus, big or narrow or closed. Sculpture lacking except growth lines and axial undulations. Aperture subcircular, inner lip whitish blue and outer lip black in colour, easily broken. Young specimens (from brood pouch) with up to 4 whorls; protoconch smooth, three primary rows of chaetae on last whorl and other whorls have two rows of chaetae. Male's testis with two or three main branches.

Cipangopaludina chinensis was the only species given a detailed description, while diagnosis characteristics are listed for all other species. All morphometric and meristic characters of *Cipangopaludina* species are given in Table 1.

Cipangopaludina ampullacea (Charpentier, 1863) (Figure 1A)

Paludina ampullacea Charpentier: Küster, 1852, *Systematisches Conchylien-Cabinet*. 2 ed.p. 23, pl. 4, fig 2–3.

Material: 25 ex. (2 female and 3 male were anatomy). KIZ 000110–000117, collected from Qiubei County, Yunnan in August 2005 by Cui GH and Du LN; KIZ 000453–000470, collected from Beihai, Tengchong County, Yunnan in April 2006 by Chen XY.

Diagnosis: shell larger, up to 53 mm, brown-greenish, with 5 whorls. Apex obtused. Spiral whorl depth is less than aperture length. Body whorl inflated, shell width about 80.1%–90.6% shell depth. Body whorl depth is less than shell width. Spiral whorls inflated and round, form a flat shoulder. Osphradium ridge-like, shorter or equal with length from anterior tip of osphradium to mantle border. The base of gill filaments wide and apex narrow and round, curve to left. Kidney arch-shape, the dorsal length of kidney right plane about 1.5 times than ventral left plane and posterior plane, and left plane and posterior plane very curve (Figure 2C-II). Vas deferens with 2 main branches and the first anterior branch with 4 parallel secondary branches. Vas deferens opens in last 1/4 of testis. Pouch filled with less than 44–48 embryos in various stages of development. Embryos with 4 whorls, body whorl with 3 chaetae and other whorls have 2 rows of chaetae.

Table 1 Morphometric and meristic characters of *Cipangopaludina* species

Species/subspecies	D	W	LA	WA	BW	N	Apex	Kidney
<i>C. lecythoides</i> (n=5)	27.3–38.8 (33.1±4.93)	23.4–32.6(27.7±3.93)	16.3–23.2(19.5±2.99)	21.6–30.5(26.1±3.74)	11.4–16.4(13.9±2.04)	4–5	pointed	unknown
<i>C. haasi</i> (n=20)	41.8–64.7(55.5±6.31)	30.4–45.9(39.8±4.34)	22.4–35.6(29.8±3.33)	31.3–48.8(41.84.85)	15.7–24.8(20.6±2.23)	6–7	pointed	Triple-shape
<i>C. leucostoma</i> (n=12)	27.4–48.9(43.0±5.85)	23.6–39.3(34.0±4.11)	16.4–28.4(24.6±3.28)	22.3–37.0(32.9±4.11)	11.6–19.3(17.3±2.17)	7	obtused	Arch-shape
<i>C. chinensis fluminalis</i> (n=25)	34.8–62.9(49.8±7.32)	26.2–47.8(38.0±4.89)	18.3–33.7(26.9±3.84)	25.5–47.0(37.2±5.17)	12.0–23.9(19.3±2.62)	6	pointed	Triple-shape
<i>C. anbryana</i> (n=28)	29.7–53.0(41.3±5.85)	23.6–41.0(33.2±4.28)	17.2–29.8(24.1±3.01)	22.4–40.1(31.9±4.29)	12.3–22.9(17.3±2.42)	5–7	pointed	Triple-shape
<i>C. lecythis ampullacea</i> (n=14)	31.6–64.2(55.8±8.17)	27.3–50.2(45.3±6.03)	18.6–38.4(31.5±4.80)	24.4–49.6(41.7±6.04)	13.4–25.4(22.4±3.07)	5	eroded	Arch-shape
<i>C. ventricosa</i> (n=23)	31.6–62.2(46.5±9.46)	26.5–49.2(38.0±6.77)	19.5–35.2(26.4±4.81)	24.7–45.3(35.2±6.49)	13.9–24.2(19.0±3.30)	6–7	pointed	Triple-shape
<i>C. chinensis</i> (n=23)	37.3–63.5(52.6±7.56)	28.5–47.9(40.2±5.68)	20.3–34.2(28.3±4.07)	27.8–46.8(38.8±5.42)	15.2–24.4(20.3±2.75)	6–7	pointed	Triple-shape
<i>C. cathayensis</i> (n=25)	27.7–58.5(41.0±7.45)	24.3–50.5(34.2±5.91)	16.9–33.3(23.7±4.09)	21.5–45.7(31.5±5.80)	12.5–24.4(17.3±2.91)	5–6	pointed	Triple-shape
<i>C. menglaensis</i> (n=10)	16.7–29.5(24.4±3.42)	13.3–22.9(19.2±2.57)	8.6–15.0(12.7±1.80)	12.0–21.3(17.8±2.61)	6.4–10.6(9.1±1.17)	5–6	pointed	unknown
<i>C. yunnanensis</i> (n=31)	15.7–28.3(20.7±3.13)	14.2–23.5(18.0±2.65)	9.4–16.7(11.9±2.00)	12.2–22.2(16.0±2.42)	6.6–13.0(9.0±1.60)	3–5	obtused	unknown
<i>C. latissima</i> (n=12)	35.0–52.8(42.7±4.89)	30.4–47.5(38.0±4.71)	20.8–33.2(25.6±4.41)	26.7–43.4(33.7±4.41)	14.9–23.5(18.2±2.27)	6	pointed	unknown
<i>C. dianchiensis</i> (n=11)	44.1–63.3(53.6±5.76)	31.8–47.2(40.2±5.00)	23.0–33.7(28.9±3.73)	32.4–45.2(39.0±4.43)	16.6–23.1(20.3±2.18)	6–7	pointed	Triple-shape
<i>C. lecythis</i> (n=6)	42.0–51.8(46.1±4.37)	32.7–39.3(36.0±2.79)	24.0–29.5(26.6±2.19)	32.5–39.6(35.5±2.97)	16.2–19.9(18.0±1.52)	6	pointed	Triple-shape
<i>C. hainanensis</i> (n=5)	30.8–38.9(33.0±3.33)	24.8–30.4(26.6±2.19)	16.3–22.1(18.4±2.19)	23.9–29.9(25.3±2.57)	12.8–15.9(14.0±1.30)	4–5	eroded	unknown
<i>C. issuriiensis</i> (n=1)	54.1	42.5	41.3	21.3	29	5	eroded	unknown

Note: Measurement values in parentheses denote mean±SE.

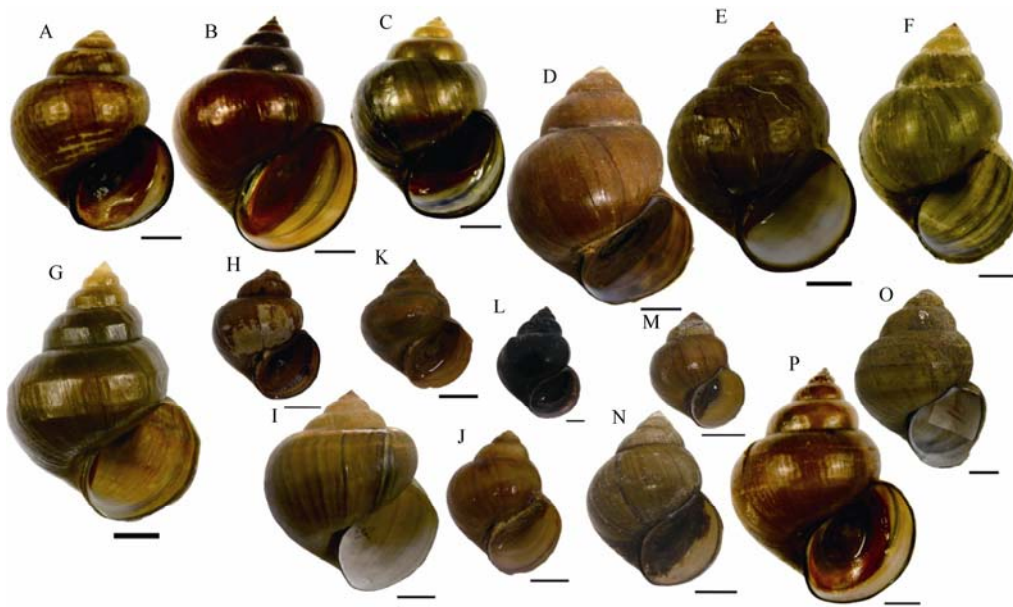


Figure 1 Shell of *Cipangopaludina*

A: *C. lecythis ampullacea*, KIZ 000453; B: *C. lecythis*, KIZ000284; C: *C. leucostoma*, KIZ 000270; D: *C. chinensis*, IOZ-FG166277; E: *C. chinensis fluminalis*, KIZ 000443; F: *C. haasi*, KIZ 000101; G: *C. dianchiensis*, KIZ 000536; H: *C. hainanensis*, IOZ-FG168161; I: *C. latissima*, IOZ-FG84656; J: *C. lecythoides*, IOZ-FG166538; K, L: *C. menglaensis*, IOZ-FG0142 (Holotype); M: *C. yunnanensis*, IOZ-FG0152 (Holotype); N: *C. aubryana*, IOZ-FG 170556; O: *C. ussuriensis*, IOZ-FG84819; P: *C. ventricosa*, KIZ000227. Scale bars=1 cm.

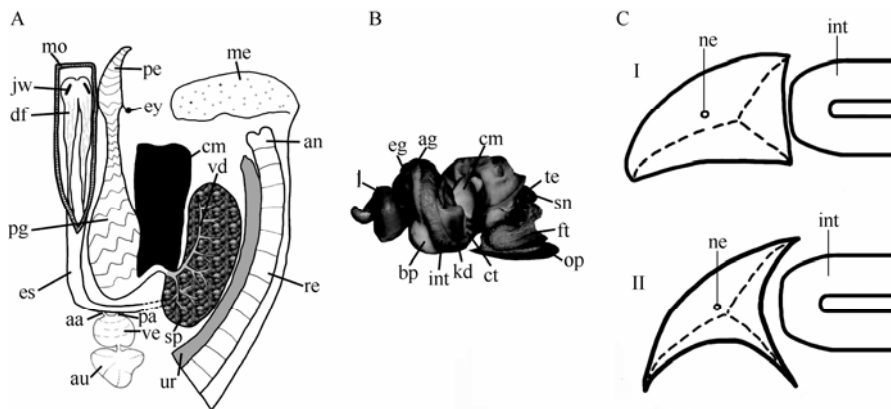


Figure 2 Anatomy and genital system of *Cipangopaludina*

A: Shell removed showing external features of animal; B: Male with mantle cavity opened mid-dorsally; C: Two type of kidney, I triple shape and II arch shape. Abbreviations: aa — anterior aorta; ag — albumen gland; an — anal papilla; au — auricle; bp — brood pouch; cm — columellar muscle; ct — ctendium; df — dorsal fold of buccal mass; eg — egg-shell gland; es — esophagus; ey — eye; ft — foot; int — intestine; jw — jaw; kd — kidney; l — liver; me — mantle edge; mo — mouth; ne — nephrostome; op — operculum; pa — posterior aorta; pe — penis; pg — prostate gland; re — rectum; sn — snout; te — tentacle; ur — ureter; ve — ventricle; vd — vas deferens.

Distribution: Southwest of China, Yunnan, Sichuan provinces and Macao (Liu, 1991).

Remarks: *Cipangopaludina ampullacea* can be distinguished from *C. chinensis*, *C. fluminalis*, *C. haasi*, *C. menglaensis*, *C. dianchiensis* and *C. ussuriensis* by spiral depth shorter than aperture depth. *Cipangopaludina ampullacea* can be distinguished from other species by the following characters: osphradium length

shorter or equal with length from anterior tip of osphradium to mantle border, vs. longer in *C. ventricosa*, *C. patris* and *C. aubryana*; shell larger, apex eroded vs. shell medium and apex pointed in *C. yunnanensis*; umbilicus small or closed vs. big and round in *C. latissima*; apex obtused vs. pointed in *C. cathayensis* and *C. lecythoides*. *Cipangopaludina ampullacea* can be distinguished from *C. lecythis* by apex eroded vs. pointed;

the upper angle of aperture acute vs. straight. However, the anatomy of *C. ampullacea* and *C. lecythis* are not obviously different, so it is suitable to treat *C. ampullacea* as a subspecies of *C. lecythis*.

***Cipangopaludina aubryana* (Heude, 1890)** (Figure 1N)

Paludina aubryana Heude, 1890, *Memoires concernant L'Histoire naturelle e L'empire chinois par des peres de la compagnie de Jesus*, 175, pl. 39.

Vivipara (chinensis) aubryana Heude, Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p 118, pl. 20, fig 6–7.

Viviparus chinensis aubryana (Heude), Yen, 1939, *Diese Arbeit erscheint gleichzeitig in den Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft Abhandlung*, 444, p. 35, taf. 3.

Viviparus chinensis aubryana (Heude), Yen, 1942, *Proceedings of the Malacological Society of London*, 190, 200, pl. 13, fig 32.

Cipangopaludina chinensis aubrayana (Heude), Pradshad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168.

Cipangopaludina lecythoides aubryana (Heude), Yen, 1943, *Nautilus*, 56(4): 124–130.

Cipangopaludina aubryana (Heude), Liu, 1991, *Proceeding of Tenth International Malacological Congress*, 590.

Materials: 20 ex. (4 females and 4 males were anatomy). IOZ–FG166735, IOZ–FG166737, from Wang County, Sichuan Province in June 1964; IOZ–FG170556, IOZ–FG170553, IOZ–FG170551, IOZ–FG 170549, from Hanshou County, Hunan province in March 1963; KIZ 000087–100, from Pu'er City, Yunnan in April 2011 by Zheng LP.

Diagnosis: shell medium, brown green, with 5 whorls. Body whorl inflated, but other whorls not, without shoulders. Apex pointed. Spiral whorl depth less than aperture depth. Osphradium ridge-like, longer than length from anterior tip of osphradium to mantle border. The base of gill filaments wide and apex narrow and pointed, does not curve to right. Kidney triple-shape, the dorsal length of kidney right plane about 1.2 times than ventral left plane, 2 times than posterior plane, the left plane and posterior plane do not curve much (Figure 2C–I). Vas deferens with 3 main branches and the first anterior branch with 4 parallel secondary branches. Vas deferens opens in last 1/3 of testis. Pouch filled with less than 10 embryos in various stages of development.

Embryos with 4 whorls, body whorl with 3 chaeta and other whorls have 2 rows of chaetae.

Distribution: Sichuan, Hunan, Guangdong, Guizhou and Yunnan Provinces, China (Liu, 1991).

Remarks: *Cipangopaludina aubryana* can be distinguished from *C. chinensis*, *C. haasi*, *C. fluminalis*, *C. dianchiensis*, *C. ussuriensis* and *C. menglaensis* by spiral depth less than aperture length and shell medium. *Cipangopaludina aubryana* can be distinguished from other species by the following characteristics: kidney triple-shape vs. arch-shape in *C. ampullacea*, *C. patris* and *C. ventricosa*; acute spiral whorl and without shoulder (vs. spiral whorl inflated and form shoulder in *C. lecythoides* and *C. yunnanensis*); shell medium and body whorl not very inflated vs. shell larger and body whorl very inflated in *C. latissima*; apex pointed, not eroded vs. apex eroded, with only 4 whorls in *C. hainanensis*; vas deferens opens in last 1/3 of testis vs. 1/4 in *C. lecythis* and *C. l. ampullacea*.

***Cipangopaludina cathayensis* (Heude, 1890)** (Figure 1C)

Paludina catayensis Heude, 1890, *Memoires concernant L'Histoire naturelle e L'empire chinois par des peres de la compagnie de Jesus*, 175, pl. 39.

Vivipara chinensis cathayensis Heude, Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p 112, pl. 18, fig 5–6.

Cipangopaludina chinensis cathayensis (Heude): Prashad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168; Yen, 1943, *Nautilus*, 56(4): 124–130.

Cipangopaludina cathayensis (Heude), Liu, 1991, *Proceeding of Tenth International Malacological Congress*, 590.

Materials: 34 ex. (2 males and 2 females were anatomy) KIZ000016–17, collected from Lake Xingyun, Yunnan in July 2008 by Du LN; KIZ000422–434, collected from Lake Dianchi, Yunnan in September 2006 by Du LN, Jiang YE and Cui GH; KIZ 000076 collected from Debao County, Guangxi in August 2009 by Yu GH and Li Y; KIZ000190–196, collected from Liaoyuan City, Jilin in October 2012 by Du LN.

Diagnosis: shell shin, medium, up to 60 mm, with 6 inflated whorls, spiral whorl with shoulder. Apex pointed. Spiral whorl depth less than aperture depth. Osphradium length similar with length from anterior tip of osphradium to mantle border, anterior 2/3 part of osphradium ridge-like and posterior 1/3 part inflated. Gill filaments same with *C. chinensis*. Kidney triple-shape. Vas defer-

ens with 3 main branches and the first anterior branch with 3–4 parallel secondary branches. Vas deferens opens in last 1/3 of testis. Female pouch filled with more than 60 embryos in various stages of development. Embryos with 3 whorls, body whorl with 3 chaeta and other whorls have 2 rows of chaetae.

Distribution: Jilin, Shanxi, Hebei, Shandong, Anhui, Jiangsu, Zhejiang, Hunan, Sichuan, Guizhou and Yunnan provinces (Liu, 1991).

Remarks: In the original description, this species was spelt *catayensis*, but later reviewers all spelt it *cathayensis*, according to the International Code of Zoological Nomenclature (1999). *Catayensis* is then treated as an inadvertent error, and thus this spelling is incorrect. *Cipangopaludina cathayensis* can be distinguished from *C. chinensis*, *C. haasi*, *C. fluminalis*, *C. dianchiensis* and *C. menglaensis* by spiral depth less than aperture depth. *Cipangopaludina cathayensis* can be distinguished from other species by the following characteristics: anterior 2/3 of osphradium ridge-like and posterior 1/3 inflated; female's pouch with more than 60 embryos, and embryo's have 3 whorls.

***Cipangopaludina chinensis* (Gray, 1834)** (Figure 1D)

Paludina chinensis Gray: in Griffith & Pidgeon, 1834, *Animal Kingdom*, pl. 1, fig 5.

Paludina chinensis Gray: Gray in Griffith & Pidgeon, 1834, *Animal Kingdom*, 599.

Vivipara chinensis (Gray), Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibungen*, p111, pl 23, fig 1.

Cipangopaludina chinensis (Gray): Prashad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168.

Viviparus chinensis chinensis (Gray): Yen, 1939, *Diese Arbeit erscheint gleichzeitig in den Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft Abhandlung*, 444, 35. Taf. 3.

Viviparus chinensis (Gray): Yen, 1942, *Proceedings of the Malacological Society of London*, 190, 200, pl. 13, fig 32.

Cipangopaludina chinensis leucostoma (Heude): Yen, 1943, *Nautilus*, 56(4): 124–130.

Cipangopaludina chinensis diminuta (Heude): Yen, 1943, *Nautilus*, 56(4): 124–130.

Bellamya (Cipangopaludina) chinensis (Gray): Smith, 2000, *Nautilus*, 114(2): 31–37.

Cipangopaludina chinensis (Heude): Prashad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168; Liu, 1991, *Proceeding of Tenth International Malacological*

Congress, 590.

Material: 40 ex. (1 males and 2 females were anatomy). IOZ-FG166277, Shangsi Co. Guangxi Province in 19th April 1974; IOZ84521, Zhaotong City, Yunnan Province in May 1932; IOZ166773, IOZ166777, Qionghai Lake, Xichang County, Sichuan Province in 4th July 1964; IOZ166733, Luofang village, Guangdong Province in March 1982; KIZ000164–165, Lake Erhai, Yunnan, collected by Du LN, Jiang YE and David Aldridge in 14 April 2006; KIZ 000294–310, Lake north mountain, Jilin City, Jilin Province, collected by Du LN on 13 October 2012; KIZ 000132–133, KIZ 000149–150, West Lake, Dali City, Yunnan, collected by Du LN in 13 April 2006, Jiang YE and Aldridge D; KIZ 000157–158, Lake Xinyun, Jiangchuan County, Yunnan, collected by Du LN, Jiang YE and Cui GH in September 2009; KIZ 000013015, KIZ 000038040, KIZ 0000363–366, KIZ 000421, Lake Dianchi, Kunming City, Yunnan, collected by Du LN and Aldridge D. in March 2006.

Description

Shell: large (up to 70 mm), oval, brown or greenish in colour, with 6–7 whorls. Apex pointed. Suture narrow. Umbilicus narrow or closed. Sculpture lacking except growth lines and axial undulations. Aperture subcircular, inner lip whitish blue and outer lip black in colour, easily brown. Young specimens (from brood pouch) with up to 4 whorls; protoconch smooth, three primary rows of chaetae on last whorl and other whorls have two rows of chaetae.

Operculum: Occupying entire shell aperture. Centre is brown and outer parts greenish. Nucleus sub-central, located closer to inner margin. Sculptured with concentric growth lines. Inner surface glossy; scar sub-circular, close to inner margin, occupying about 2/3 of opercula area.

External morphology (Figure 2B): head and foot black. Snout cylindrical, anterior margin flat. Length of tentacles about 1.3 times longer than snout length, base at side of snout base. Ommatophore short, located between basal and middle third of outer surface of each tentacle. Foot large, sole simple. Opercular pad larger than its base in dorsal foot surface. Columellar muscle thick.

Radula: Central tooth with wide rounded major denticles and 4 smaller triangular denticles on each side. Lateral tooth with tongue-shaped major denticles and 3 minor denticles on each side. Inner marginal tooth with

tongue-shape major denticles and 3 minor denticles and marginal teeth with 10 almost equal-sized denticles.

Mantle organs (Figure 2A-B): Mantle border simple and thick. Osphradium ridge-like, very close to ctenidium, about same length from anterior tip of osphradium to mantle border. Ctenidium long and narrow, about same length as pallial cavity, anterior end at mantle border. Gill filaments very tall and narrow, arched towards right and apex slightly pointed, close to food groove.

Hypobranchial gland lies on left of gill margin. Right margin of mantle cavity filled by oviduct in females. Ureter runs along mantle cavity right margin in males or edging oviduct in females. Rectum on dorsal and left sides of ureter. At right end of mantle border, in females, presenting three openings, most posterior and smaller is ureter pore, anus most anterior, and female pore larger, located between anus and ureter pore.

Alimentary canal: Oval mouth, bounded by fleshy lips, ventral at anterior end of snout. Jaw plates ridge-like (Figure 2A). Esophagus with pair of dorsal, longitudinal folds, about 1.5 times of buccal mass length. Esophagus runs along the hypobranchial gland to posterior of columellar muscle, and then turns right and passes upwards in floor of pericardial chamber to reach digestive gland in upper part of visceral hump where it curves round to open into stomach. Stomach located halfway posterior to pallial cavity, posterior half immersed in digestive gland. Esophagus is inserted in posterior gastric extremity, and as gradually enlarges curves towards left. After this curve, stomach abruptly expands becoming almost as wide as whorl, posterior narrowing, without clear separation with intestine. Intestine forms loop overlying pericardial cavity and when it reaches digestive gland turns sharply forwards to continue as rectum. Rectum passes forwards on right of mantle cavity to open at anus lying just behind mantle edge.

Circulatory and excretory systems: Heart located at anterior ventral of kidney. Auricle connected with ctenidial vein just posterior to gill. Ventricle posteriorly connected to auricle by a thin tube. The size of ventricle is same as the auricle. Kidney triangular (Figure 2 C-I), with four almost plane surfaces: 1) posterior surface towards pericardium; 2) left with pallial cavity; 3) ventral right with ureter; 4) dorsal with mantle. The dorsal length of the kidney's left plane is similar to the ventral right plane, and about two times longer than

posterior plane. Nephrostome is a round, small pore, located in centre basally inferior region of ventral surface of kidney. Ureter runs between rectum and oviduct (in females) or right pallial cavity edge (in males). Ureter pore just posterior to anus (or just posterior to female pore).

Genital system.

Male (Figure 2A): Testis compact, semi-lunar, on right of mantle cavity. Extends to upper end of mantle cavity, where apex close to pericardial cavity also connected by thin fold of membrane with lower surface of digestive gland. Testis flattened laterally, right surface abuts columellar mussel while left surface abuts right wall of ureter. Vas deferens very narrow, running on columellar and inferior ventral margin of testis, with 2 main branches, and in the anterior branch with 5–6 parallel secondary branches, the branches with many very narrow branches from different portions of testis. Vas deferens opens in last 1/3 of testis and runs to prostate gland in mantle cavity along mantle cavity floor for about 3/4 of its length; left 1/4 length of vas deferens abruptly narrows and is surrounded by very thick, muscular walls. Vas deferens runs all along the right cephalic tentacle, its inner surface relatively broad, with some inner, longitudinal folds. Vas deferens opens in tentacle tip as broad papilla with rounded tip. Right tentacle possesses deep concavity located at right from genital papilla. Papilla can retract into its concavity.

Female. Ovary grey, located in same position as testis. Ovary in close contact with posterior wall of cardiac region of stomach and along course of hepatic artery. Oviduct very narrow; from albumen gland it runs to posterior end of columella, and then turns left, making a loop. Oviduct increases in size and runs to capsule gland along brood pouch. Brood pouch located in dorsal of oviduct. Albumen gland tongue-shaped, slightly curved, capsule gland on dorsal and posterior surface and opens to brood pouch. Walls of brood pouch thin, semi-transparent, smooth. Pouch filled with about 45–84 embryos in various stages of development.

Ecology and habitat: it lives in slow-moving water such as lakes, pond, irrigation canals, ditches and slow moving stream (Pace, 1973). It is a benthic grazer and filter feeder, feeding on benthic and epiphytic diatom (Plinski et al, 1978), often found on sandy to muddy substrates.

Distribution: original range in China (including Taiwan), Korea, and Japan, but has also been introduced

in freshwater ponds and lakes in Canada, the north-eastern USA, and Europe (Soes et al, 2011).

Remarks: Although Yen (1943) mentioned that *C. leucostoma* (Heude) and *C. diminuta* (Heude) are synonymous with *C. chinensis* (Gray), the authors thought these two species are synonymous with *C. patris* (Kobelt) according to apex obtuse and less than 6 whorls. Additionally, *Cipangopaludina wingatei* (Smith) could be synonymous with *C. chinensis* according to shell size, spiral depth longer than length of aperture, and number of whorls. *Cipangopaludina chinensis*, *C. dianchiensis*, *C. fluminalis*, *C. haasi*, *C. ussuriensis* and *C. menglaensis* share the characteristic that spiral depth is longer than length of the aperture. However, *C. chinensis* can be distinguished from *C. dianchiensis* and *C. ussuriensis* by its shell smooth rather than having a shell with a ridge; female's pouch has more than 80 embryos vs. less than 10 embryos in *C. dianchiensis*; embryo with three primary rows of chaetae on last whorl vs. 3 ridges in *C. dianchiensis*. *Cipangopaludina chinensis* can be distinguished from *C. fluminalis* by the following characters: shell thin vs. thick, umbilicus close vs. big and deeply.

***Cipangopaludina dianchiensis* Zhang, 1990** (Figure 1F)

Cipangopaludina dianchiensis Zhang, 1990, *Acta Zootaxonomica Sinica*, 15(1): 25–27.

Materials: 34 ex. (2 males and 3 females were anatomy). KIZ 000233, collected in November 2002 by Cui GH; KIZ 000001–KIZ 000004, collected in June 2008 by Du LN, Jiang YE and Barclay H; KIZ 000005–KIZ 000012, collected in September 2005 by Du LN and Aldridge D; KIZ 000212–KIZ 000217, KIZ 000287–KIZ 000293; KIZ 000311–KIZ 000316, collected in January 2006 by Du LN and Yuan C; KIZ 000373, KIZ 000231 collected in June 2006 by Du LN. All specimens were from Lake Dianchi.

Diagnosis: shell thick. Body whorl with 7–12 ridges (3–4 ridges clearly). Apex pointed. Osphradium ridge-like, shorter than length from anterior tip of osphradium to mantle border. Gill filaments and jaw plate are the same as *C. chinensis*. The size of ventricle is the same as the auricle. Vas deferens has 3 main branches and the first anterior branch has 4 “V” shaped secondary branches. Vas deferens opens in last 1/3 of testis. Pouch filled with about 6–8 embryos in various stages of development. Embryos with 5 whorls, body whorl with 3 ridges and other whorls with 1 ridge.

Distribution: only known to live in Lake Dianchi, Yunnan.

Remark: Morphology characteristics, such as shell thickness, body whorl with clear ridges, female's pouch with few (6–8) embryos and embryo shell with ridges can be distinguished clearly from other species of genus *Cipangopaludina*. Additionally, phylogenetic analysis indicated that *C. dianchiensis* clustered with species of *Margarya* in Lake Dianchi (Du et al, 2013). The morphology and molecular results indicated that *C. dianchiensis* should be placed into the genus *Margarya*.

***Cipangopaludina fluminalis* (Heude, 1890)** (Figure 1E)

Paludina fluminalis Heude, 1890, *Memoires concernant L'Histoire naturelle e L'empire chinois par des peres de la compagnie de Jesus*, 175, pl. 39.

Vivipara chinensis fluminalis Heude, Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p 116, pl. 19, fig. 4–5.

Viviparus chinensis fluminalis (Heude), Yen, 1939, *Diese Arbeit erscheint gleichzeitig in den Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft Abhandlung*, 444, p. 35, taf. 3; Yen, 1942, *Proceedings of the Malacological Society of London*, 190, 200, pl. 13, fig 32.

Cipangopaludina chinensis fluminalis (Heude), Prashad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168.

Cipangopaludina lecythoides fluminalis (Heude): Yen, 1943, *Nautilus*, 56(4): 124–130.

Cipangopaludina fluminalis (Heude), Liu, 1991, *Proceeding of Tenth International Malacological Congress*, 590.

Materials: 21 ex (1 male and 1 female were anatomy). KIZ 000181 collected from Jinping County, Honghe prefecture, Yunnan in April, 2011 by Jiang WS; KIZ 000204–000211 collected from West Lake, Dali prefecture, Yunnan in April 2006 by Du LN, Jiang YE and Aldridge D; KIZ 000384 collected from Songming County, Kunming prefecture, Yunnan in December 2005 by Du LN; KIZ 000442–000451 collected from Songming County, Kunming prefecture, Yunnan in December 2004 by Du LN.

Diagnosis: shell is thick, larger, up to 60 mm, with 7 slightly inflated whorls. Apex pointed. Spiral whorl depth longer than aperture depth. Umbilicus big and deep. Osphradium length similar with length from anterior tip of osphradium to mantle border. Gill filaments same as *C.*

chinensis. Kidney triple shaped, the dorsal length of kidney left plane about same length as ventral right plane, 1.5 times longer than posterior plane. Vas deferens with 3 main branches and the first anterior branch with 5–6 parallel main secondary branches. Vas deferens opens in last 1/3 of testis. Pouch filled with 12 embryos in various stages of development. Embryos with 4 whorls, body whorl with 3 chaeta and other whorls have 2 rows of chaetae.

Distribution: Yangtze River (Yen, 1943; Liu, 1991).

Remarks: *Cipangopaludina fluminalis* is very similar with *C. chinensis* except the shell thick rather than thin; umbilicus big and deep rather than small or closed. The anatomy characteristics were relatively similar with little difference, making it is possible to treat *C. fluminalis* as subspecies of *C. chinensis*.

***Cipangopaludina latissima* (Dautzenberg et H. Fischer, 1905)** (Figure 1I)

Paludina lecythoides latissima Dautzenberg et H. Fischer, 1905, *Journal de Conchylogie*, p418, pl. 10, fig 17; Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibungen*, p 144, pl. 29, fig 1.

Cipangopaludina lecythoides latissima (Dautzenberg et H. Fischer), Pradshad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168.

Cipangopaludina latissima (Dautzenber et H. Fischer): Yen, 1943, *Nautilus*, 56(4): 124–130; Liu et al, 1991, *Proceeding of Tenth International Malacological Congress*, 590.

Materials: 15 shell specimens. IOZ-FG84653–84667, collected from Mengzi County, Yunnan in March 1927.

Diagnosis: shell is large, round, up to 53 mm, with 6 whorls. Apex pointed. Body whorl very inflated, shell width is about 85%–95% of shell depth. Due to the body whorl inflated, the upper of body whorl has a flat shoulder. Aperture ellipse. Umbilicus very big, round. Anatomy characteristics unknown.

Distribution: only known to be from Mengzi County, Yunnan.

Remarks: *Cipangopaludina latissima* can be distinguished from other species of *Cipangopaludina* by the body whorl special inflated, and the upper of body whorl with a flat shoulder.

***Cipangopaludina lecythoides* (Benson, 1842)** (Figure 1J)

Paludina lecythoides Benson, 1842, *The Annals and Magazine of Natural History, Zoology, Botany and Geology* 9, 488; Philippi, 1846, *Abbildungen und Beschrei-*

bungen neuer oder wenig gekannter Conchylien herausgegeben, II. p.133, pl 2, fig 1; Küster, 1852, In *Abbildungen nach der Natur mit Beschreibungen. Systematisches Conchylien-Cabinet* 2ed, p. 23, pl. 5, fig 1, 2; Reeve, 1862, *Conchologia iconica, or, illustrations of the shell of molluscous animals*, pl. 4, fig 21; Dautzenberg et H. Fischer, 1905, *Journal de Conchylogie*, p417–418.

Paludina (Vivipara) lecythoides Benson: Mabille et Le Mesle, 1866, *Journal de Conchyliologie*, p. 134; Fischer, 1891, *Catalogue et Distribution géographique des Mollusques terrestres, fluviatiles et marins d'une partie de l'Indo-Chine (Siam, Laos, Cambodge, Conchinchine, Annam, Tonkin)*, p. 177.

Vivipara (chinensis var.) lecythoides (Benson), Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibungen*, p 119, pl. 23, fig 8.

Cipangopaludina chinensis lecythoides (Benson), Prashad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168.

Cipangopaludina lecythoides (Benson), Yen, 1943, *Nautilus*, 56(4): 124–130; Liu et al, 1991, *Proceeding of Tenth International Malacological Congress*, 590.

Materials: 1 ex. KIZ 000507, collected from Hangzhou City, Zhejiang Province in April 2013 by Lu HF;

Diagnosis: shell depth 55 mm, with 6 inflated whorls. Shell dark brown, with clearly growth lines. Apex pointed. Spiral whorl depth shorter than aperture depth. Umbilicus small, nearly closed. Vas deferens has 2 main branches and the first anterior branch with 3 parallel secondary branches. Vas deferens opens in last 1/3 of testis.

Distribution: Zhejiang Province.

Remarks: Although Wang & Xie (2005) mentioned that this species is distributed in Yunnan, it was not collected during field excursions undertaken between 2003–2008 by authors Du LN and Chen XY. Generally, the validity of this species is unclear, as it is difficult to distinguish *C. lecythoides* and *C. cathayensis* by shell morphology alone. Further anatomic characteristics are required to determine the validity of this species.

***Cipangopaludina lecythis* (Benson, 1836)** (Figure 1B)

Paludina lecythis Benson, 1836, *Journal of Asiatic Society of Bengal*, 5: 745.

Paludina chinensis lecythis Benson: Nevill, 1885, *Hand list of Mollusca in the Indian Museum: Gastropoda. Prosobranchia–Neurobranchia*, p. 20.

Paludina ampullacea Reeve (not Charpentier), 1862, *Conchologia iconica, or, illustrations of the shell of*

molluscos animals, 12.

Vivipara lecythis Benson, Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p 148, pl. 30, fig 1–2.

Cipangopaludina chinensis lecythis (Benson): Prashad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168.

Cipangopaludina lecythis (Benson): Yen, 1943, *Nautilus*, 56(4): 124–130; Liu et al, 1991, *Proceeding of Tenth International Malacological Congress*, 590.

Materials: 25 ex. (1 female and 2 males). KIZ 000018–000030 collected from Songming County, Kunming City, Yunnan in April 2006 by Du LN and Yuan C; KIZ 000044 collected from Lake Dianchi, Yunnan in April 2006 by Du LN and Yang J; KIZ 000144 collected from Lake Erhai in April 2006 by Du LN, Yang YE and Aldridge D; KIZ 000151–156 collected from Lake Xingyun, Yunnan in September by Du LN, Jiang YE and Cui GH; KIZ 000224 collected from Lake Xingyun, Yunnan in April by Du LN; KIZ 000284–286 collected from Lake Dianchi, Yunnan in March 2006 by Du LN.

Diagnosis: shell larger, up to 60 mm, brown greenish, with 7 whorls. Apex pointed. Spiral whorl depth shorter than aperture depth. Whorls inflated, with a shoulder. Aperture ellipse, the upper of aperture form a straight shoulder. Umbilicus small or closed. Osphradium ridge-like, shorter than length from anterior tip of osphradium to mantle border. Gill filaments same with *C. chinensis*. Vas deferens with 2 main branches and the first anterior branch with 4 parallel secondary branches. Vas deferens opens in last 1/4 of testis. Pouch filled with about 37 embryos in various stages of development. Embryos with 3–4 whorls, body whorl with 2 chaetae and other whorls with 1 chaetae.

Distribution: Yunnan, China. Burma (Kobelt, 1909).

Remarks: *Cipangopaludina lecythis* can be distinguished from other species of this genus by its special aperture shape, the upper of aperture straight and form a flat shoulder. Kobelt (1909) list *C. lecythis ampulliformis* (Souleyet) as a subspecies of *C. lecythis*, which are distributed in both Burma and Yunnan, China. According to Kobelt (1909) it is difficult to distinguish between these two species, so we opted to treat *C. lecythis ampulliformis* as synonymous with *C. lecythis*.

***Cipangopaludina patris* (Kobelt, 1906)** (Figure 1C)

Paludina patris Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p 118, pl. 23, fig 4–5.

Cipangopaludina chinensis patris (Kobelt), Prashad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8:

168.

Cipangopaludina lecythoides (Heude, non Benson): Yen, 1943, *Nautilus*, 56(4): 124–130.

Cipangopaludina compacta (Kobelt, non Nevill): Yen, 1943, *Nautilus*, 56(4): 124–130.

Cipangopaludina lecythis crassior Annandale: Yen, 1943, *Nautilus*, 56(4): 124–130.

Materials: 28 ex (2 females and 2 males were anatomy). KIZ 000268–000279, collected from Yuanjiang County, Yunnan in January 2010 by Du LN; KIZ 000369–000372, collected from Jinning County, Yunnan in August 2006 by Du LN; KIZ 000391–000402, collected from Yuanjiang County, Yunnan in January 2013 by Du LN.

Diagnosis: shell medium, up to 50 mm, brownish, with 6 whorls. Apex obtuse. Whorls inflated, especially last two whorls, upper three whorls slightly inflated and always eroded. Spiral whorl depth shorter or equal with aperture depth. Aperture ellipse. Umbilicus closed. The shape of the kidney is similar with *C. ampullacea*. Osphradium ridge-like, longer than length from anterior tip of osphradium to mantle border. Gill filaments same with *C. chinensis*. Vas deferens with 3 main branches and the first anterior branch with 1 “V” shape and 3 parallel secondary branches. Vas deferens opens in last 1/3 of testis. The loop of oviduct exceeds the posterior margin of columellar muscle. Pouch filled with 96–109 embryos in various stages of development. Embryos with 3 whorls, body whorl with 3 chaetae and other whorls with 2 chaetae.

Distribution: Yunnan, Guangdong and Zhejiang provinces, China.

Remarks: *Cipangopaludina patris* can be distinguished from *C. chinensis*, *C. haasi*, *C. dianchiensis*, *C. ussuriensis* and *C. menglaensis* by a spiral depth shorter than aperture length and a medium shell. *Cipangopaludina patris* can be distinguished from other species by the following characteristics: larger shell, up to 50 mm (vs. medium, up to 26 mm in *C. yunnanensis*); the kidney arch-shape is similar with *C. ampullacea*, (vs. triple-shape in *C. cathayensis*, *C. aubryana* and *C. lecythoides*); medium shell and body whorl are not very inflated (vs. shell larger and body whorl very inflated in *C. latissima*); shell with 6 whorls (vs. only with 4 whorls in *C. hainanensis*); the upper of aperture without straight shoulder (vs. with straight shoulder in *C. lecythis*).

***Cipangopaludina haasi* (Prashad, 1928)** (Figure 1F)

Cipangopaludina chinensis haasi Prashad, 1928,

Memoirs of the Indian Museum, Calcutta, 168.

Paludina longispira Heude, 1890, *Memoires concernant L'Histoire naturelle e L'empire chinois par des peres de la compagnie de Jesus*, 175, pl. 39.

Vivipara chinensis longispira Heude, Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p 115, pl. 19, fig 3.

Viviparus chinensis longispira (Heude), Yen, 1939, *Diese Arbeit erscheint gleichzeitig in den Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft Abhandlung*, 444, p. 35, taf. 3.

Viviparus chinensis longispira (Heude), Yen, 1942, *Proceedings of the Malacological Society of London*, 190, 200, pl. 13, fig 32.

Cipangopaludina haasi (Prashad): Yen, 1943, *Nautilus*, 56(4): 124–130.

Cipangopaludina longispira (Heude), Liu, 1991, *Proceeding Tenth International Malacological Congress*, 590.

Materials: 44 ex (2 females and 2 males were anatomy). KIZ 000197–000198, KIZ 000280–000282, collected from Black dragon spring, Songming Town, Kunming, Yunnan in December 2004 by Cui GH and Chen XY; KIZ 000122–131, collected from Xiayu Village, Zhangshu City, Jiangxi Province in February 2006 by Yu GH; KIZ 00101–00108, collected from Lake Yilong, Yunnan in February 2008 by Du LN and Jiang YE; KIZ 000477–000497, collected from Hangzhou City, Zhejiang Province in April 2013 by Lu HF.

Diagnosis: shell larger, up to 65 mm, greenish, with 7 whorls. Apex pointed. Suture shallow. Spiral whorl depth higher than aperture depth. Shell width less than body whorl depth. Whorls slightly inflated, do not form shoulder. Umbilicus small. Aperture ellipse. Osphradium ridge-like, longer than the length from anterior tip of osphradium to mantle border. Gill filaments same as *C. chinensis*. Esophagus has pair of dorsal, longitudinal folds, about 2 times of buccal mass length. Stomach elliptical, spoon-shape. Heart located anterior ventral of kidney. Ventricle is about 2 or 3 times larger than auricle. Kidney triple-shape. Nephrostome round, small pore, located in posterior 1/5 of ventral surface of kidney. Vas deferens with 2 main branches and the first anterior branch has 8 to 9 parallel secondary branches. Vas deferens opens in last 1/4 of testis. Female's pouch length is about 4 times longer than egg gland. Pouch filled with 128–188 embryos in various stages of development. Embryos with 4 whorls, body whorl with 3 chaetae and other whorls with 2 chaetae.

Distribution: Hunan, Jiangxi, Sichuan, Zhejiang and Yunnan Provinces, China.

Remarks: *Cipangopaludina haasi*, *C. dianchiensis*, *C. chinensis*, *C. ussuriensis* and *C. menglaensis* share the characteristic that spiral depth is longer than length of the aperture. However, *C. haasi* could be distinguished from *C. dianchiensis* and *C. ussuriensis* by shell smooth vs. shell with ridge; female's pouch with more than 128–188 embryos vs. less than 10 embryos in *C. dianchiensis*; embryo with three primary rows of chaetae on last whorl vs. 3 ridges in *C. dianchiensis*. *Cipangopaludina haasi* could be distinguished from *C. chinensis* by the following characteristics: body whorl not inflated vs. inflated; body whorl depth same or shorter than body width vs. obviously longer. *Cipangopaludina haasi* could be distinguished from *C. menglaensis* by a larger shell, up to 65 mm vs. smaller, up to 30 mm; body whorl not inflated vs. inflated.

***Cipangopaludina hainanensis* (Möllendorff, 1909)** (Figure 1H)

Vivipara (*chinensis* var.) *hainanensis* Möllendorff, in Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p 117, pl. 19, fig. 6–7.

Cipangopaludina chinensis hainanensis (Möllendorff): Prashad, 1928, *Memoirs of the Indian Museum, Calcutta*, 168.

Cipangopaludina hainanensis (Möllendorff): Yen, 1943, *Nautilus*, 56(4): 124–130.

Materials: 5 ex. (without specimens were anatomy). IOZ–FG 168660 collected from Ledong County, Hainan Island in December 1989; IOZ–FG 168160–168163 collected from Chang Jiang County, Hainan Island in December 1989.

Diagnosis: shell medium, up to 40mm. Apex eroded, left 4–5 inflated whorls. Suture deeply. Umbilicus big and deep.

Distribution: only known from Hainan Island.

Remarks: this species was evaluated as being extinct by Wang and Xie (2005). Existing specimens can be distinguished from other species by medium shell, apex eroded, with 4–5 inflated whorls and umbilicus big and deep.

***Cipangopaludina menglaensis* Zhang, Liu et Wang, 1981** (Figure 1L)

Cipangopaludina menglaensis Zhang, Liu et Wang, 1981, *Acta Zootaxonomica Sinica*, 6(1): 40.

Materials: 10 ex. IOZ–FG 0142 (holotype), IOZ–FG 00143–151 (Paratypes) from Manzhazai Village,

Pu'er City, Yunnan in March 1965 by Zhang WZ and Liu YY.

Diagnosis: shell dark brown, small, up to 30 mm, with 6 whorls. Apex pointed. Suture deeply. Central tooth with wide rounded major denticles and 3 or 4 smaller triangular denticles on each side. Lateral tooth with tongue-shaped major denticles and 4 or 5 minor denticles on each side. Inner marginal tooth with tongue-shape major denticles and 3 or 4 minor denticles and marginal teeth with 20 almost equal sized denticles.

Distribution: only known from type locality.

Remarks: Without anatomized specimens, the anatomy characteristics remain unknown. However, this species can be distinguished from other species of *Cipangopaludina* by a smaller shell, up to 30 mm and marginal teeth with 20 almost equal sized denticles.

***Cipangopaludina ussuriensis* (Gerstfeldt, 1859)** (Figure 10)

Paludina ussuriensis Gerstfeldt, 1859, *Memoires des savants Strangers*, 9: 507, fig 1–4; Reeve, 1862, *Conchologia iconica, or, illustrations of the shell of molluscous animals*, pl. 8, fig 1–4;

Vivipara ussuriensis (Gerstfeldt), Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p108, pl. 18, fig 1–4.

Cipangopaludina ussuriensis (Gerstfeldt), Yen, 1943, *Nautilus*, 56(4): 124–130; Liu *et al.*, 1991, Proceeding Tenth International Malacological Congress, 590.

Material: 1 ex. IOZ-FG84819, collected from Khanka Lake, Heilongjiang Province in 1960.

Diagnosis: shell larger, up to 54 mm, brown–greenish, with 6 whorls and two or three brown band. Apex obtuse. Spiral depth longer than aperture depth. Shell width is about 78.5% shell depth. Body whorl with 4 clear ridges, other whorls with 2 ridges. Umbilicus small.

Distribution: Lower Amur River.

Remarks: *Cipangopaludina ussuriensis* can be distinguished from other species of this genus by the following character: apex obtuse, body whorl with 4 ridges and other whorl with 2 ridges.

***Cipangopaludina ventricosa* (Heude, 1890)** (Figure 1P)

Paludina ventricosa Heude, 1890, *Memoires concemant L'Histoire naturelle e L'empire chinois par des peres de la compagnie de Jesus*, 175, pl. 39.

Vivipara chinensis ventricosa (Heude): Kobelt, 1909, *Abbildungen Nach de Natur mit Beschreibngen*, p 114, pl. 19, fig 1–2.

Cipangopaludina chinensis ventricosa (Heude), Pradshad, 1928, *Memoirs of the Indian Museum, Calcutta*, 8: 168.

Cipangopaludina ventricosa (Heude), Yen, 1943, *Nautilus*, 56(4): 124–130; Liu, 1991, Proceeding Tenth International Malacological Congress, 590.

Materials: 24 ex. (1 female and 2 males were anatomy). KIZ 000031 collected from Yangguang County, Yunnan in February 2006 by Du LN; KIZ 000036–38, KIZ 000174, KIZ 000227–228, KIZ 000230 collected from Lake Dianchi, Yunnan in March 2006 by Du LN; KIZ 000143 collected from Lake Erhai, Yunnan in April 2006 by Du LN, Jing YE and Aldridge A; KIZ 000175–180 collected from Jiuzai dragon spring, Yunnan in March 2006 by Du LN; KIZ 000226 collected from Lake Xingyun, Yunnan in April 2006 by Du LN; KIZ 000283 collected from Black dragon spring, Songming County, Yunnan in December 2004 by Cui GH and Chen XY; KIZ 000361–362 collected from Black dragon spring, Songming County, Yunnan in December 2005 by Du LN; KIZ 000437–441 collected from Black dragon spring, Songming County, Yunnan in April 2006 by Du LN.

Diagnosis: shell larger, medium thick, up to 65 mm, with 7 whorls. Body whorl inflated. Aperture inflated and round, but the upper angle does not forms a straight shoulder. Apex pointed. Umbilicus big and deep. Osphradium ridge-like, longer than length from anterior tip of osphradium to mantle border. Gill filaments same with *C. chinensis*. The dorsal length of kidney left plane about same length with ventral right plane, 1.5 times than posterior plane. Vas deferens with 3 main branches and the first anterior branch with 1 “V” shape and 3 parallel secondary branches. Vas deferens opens in last 1/4 of testis. Pouch filled with 33 embryos in various stages of development. Embryos with 3 whorls, body whorl with 3 chaetae and other whorls with 2 chaetae.

Distribution: Yunnan, Sichuan and Guizhou Provinces, China (Liu, 1991).

Remarks: *Cipangopaludina ventricosa* is similar to *C. cathayensis* and *C. ampullacea* with a slightly larger shell, apex pointed and whorls inflated. However, *C. ventricosa* can be distinguished from *C. cathayensis* by following characteristics: shell with 7 whorls *vs.* 6; aperture round *vs.* ellipse; Osphradium ridge-like, longer than length from anterior tip of osphradium to mantle border *vs.*, anterior 2/3 part of osphradium ridge-like and posterior 1/3 part inflated, osphradium length similar

with length from anterior tip of osphradium to mantle border; Vas deferens opens in last 1/4 of testis vs. 1/3. *Cipangopaludina ventricosa* can be distinguished from *C. ampullacea* by the following characteristics: upper aperture does not form straight shoulder vs. having a straight shoulder; umbilicus big and deep vs. closed; Osphradium longer than length from anterior tip of osphradium to mantle border vs. shorter; Vas deferens opens in last 1/4 of testis vs. 1/3.

***Cipangopaludina yunnanensis* Zhang, Liu et Wang, 1981** (Figure 1M)

Cipangopaludina menglaensis Zhang, Liu et Wang, 1981, *Acta Zootaxonomica Sinica*, 6(1): 40–41.

Materials: 48 ex. IOZ–FG 0152 (holotype), IOZ–FG164354–164400 (Paratypes) from Maliping village, Pu'er City, Yunnan in May 1957 by Zhang WZ and Liu YY.

Diagnosis: shell greenish, small, up to 26 mm, with 5 whorls. Apex obtuse. Shell surface with conspicuous growth lines and irregular malleation. Central tooth with wide rounded major denticles and 3 or 4 smaller triangular denticles on each side. Lateral tooth with tongue-shaped major denticles and 3 or 5 minor denticles on each side. Inner marginal tooth with tongue-shape major denticles and 3 or 4 minor denticles and marginal teeth with 13 almost equal-sized denticles.

Distribution: only known from type locality.

Remarks: Without anatomized specimens, the anatomy characters remain unknown. However, it can be distinguished from other species of *Cipangopaludina* by a smaller shell, up to 30 mm and marginal teeth with 13 almost equal-sized denticles.

Morphometric analysis by PCA

The five shell characteristics are shown in Table 1. The first two factors PCA accounted for 85.4% of the total variance (Table 2). The first factor (55.9% of the variation of the selected variables) separated the ratios W/D, BW/D, BW/LA and BW/WA (factor loadings >80). The second factor (29.5% of the variation of the selected variables) separated the WA/D and WA/LA. A scatter map was made by averaging the first and second PCA factors per species (Figure 3). In PCA 1 axis (X-axis), W and BW are positively, D and LA negatively related to X-axis, respectively. In PCA 2 axis (Y-axis), WA is positive, D and LA negatively related to Y-axis, respectively. These variances are related to the shape of

aperture and body whorl depth. The pot of *C. latissima* located in the right of region II, it indicated that this species has a taller body whorl and shell width, but has a shorter spiral whorl. To the contrary, *C. haasi* looks slimmer due to taller spiral whorl and smaller shell width.

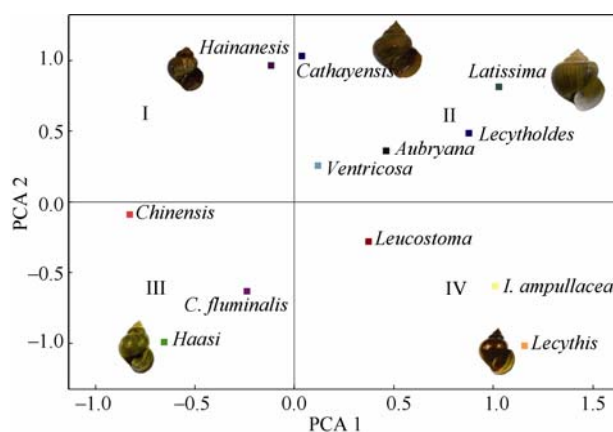


Figure 3 Scatterplots of scores on 1st and 2nd principle components of Chinese *Cipangopaludina*

Table 2 Loadings of the first two principal components for 5 shell characteristics of Chinese *Cipangopaludina* species

	PCA 1	PCA 2
W/D	0.832*	0.322
LA/D	0.571	0.513
WA/D	0.397	0.914*
BW/D	0.949*	0.288
WA/LA	0.078	0.858*
BW/LA	0.856*	0.001
BW/WA	0.727*	-0.682
Prp. Total	55.9	29.5

* loadings > 0.80.

Additionally, *C. haasi*, located in left bottom of region III, has an oval aperture. *Cipangopaludina hainanensis* and *C. cathayensis* located in the top of region I and II, they have a bigger WA and relatively smaller LA, indicating these two species have a round aperture.

Key to species of Chinese *Cipangopaludina*

- 1 Shell with brown color band and ridge *C. ussuriensis*
- Shell without brown color band or ridge 2
- 2 Apex pointed 3
- Apex obtuse or eroded 11
- 3 The upper of body whorl form a flat shoulder *C. latissima*

- The upper of body whorl without a flat shoulder.....4
- 4 Shell with 5 whorls, spiral whorl not inflated
..... *C. aubryana*
- Shell with 6–7 whorls, and spiral whorl inflated5
- 5 Vas deferens opens in last 1/3 of testis.....6
- Vas deferens opens in last 1/4 of testis.....10
- 6 The first anterior branch of vas deferens with more
than 5 secondary branches7
- The first anterior branch of vas deferens with less than
3 secondary branches9
- 7 Shell width shorter than body whorl depth; the first
anterior branch of vas deferens with 8 secondary
branches*C. haasi*
- Shell width longer than body whorl depth; the first ant-
erior branch of vas deferens with 5–6 secondary bran-
ches8
- 8 Shell thin; umbilicus small, nearly closed
..... *C. chinensis*
- Shell thick; umbilicus big and deeply*C. c. fluminalis*
- 9 Vas deferens with 3 main branches..... *C. cathayensis*
- Vas deferens with 2 main branches.....*C. lecythoides*
- 10 Vas deferens with 2 main branches; kidney triple
shape..... *C. lecythis*
- Vas deferens with 3 main branches; kidney arch shape
.....*C. ventricosa*
- 11 Shell medium, with 4–5 whorls..... *C. hainanensis*
- Shell larger, with 6 whorls12
- 12 Vas deferens with 2 main branches, opens in last 1/4 of
testis..... *C. l. ampullacea*
- Vas deferens with 3 main branches, opens in last 1/3
of testis *C. leucostoma*

DISCUSSION

Alongside numerous difficulties in determining the validity of numerous *Cipangopaludina*—lack of anatomy samples, discrepancies in the literature, or ambiguous morphological data—the genus itself is also problematic. Smith (2000) treated *Cipangopaludina* as subgenus of *Bellamya*, while Sengupta et al (2009) indicated that species of *Bellamya* from Asia could not belong to this genus. In China, there are currently seven recognized genera of Bellamyinae recorded, viz. *Margarya* Nevill, 1877, *Cipangopaludina* Hannibal, 1912, *Bellamya* Jousseaume, 1886, *Mekongia* Crosse et Fischer, 1876, *Filopaludina* Habe, 1964, *Angulyagra* Benson, 1836 and *Trochotaia* Brandt, 1974 (Liu et al, 1979, 1993; Du et al, 2011). Generally speaking, it is possible to distinguish

these, as the shell of *Cipangopaludina*, *Margarya*, and *Trochotaia* tend to be larger, while other four genera species are more mid-sized. Similarly, species of *Filopaludina* and *Mekongia* have a color band, and *Angulyagra* has ridges. For more detailed markers, *Cipangopaludina* can be distinguished from *Trochotaia* by shell round or oval vs. depressed pyramidally, last whorl with a sharp keel, and from *Margarya* by shell smooth vs. shell with ridges, nodules or spines; embryo with chaetae vs. ridges or nodules. Based on these criteria, we opted to treat *Cipangopaludina* as a valid genus.

Generally, the diagnostic characteristics of *Cipangopaludina* are shell median to large, sculpture lacking except growth lines and axial undulations. Aperture subcircular. Young specimens (from brood pouch) with up to 3–4 whorls; protoconch smooth, three primary rows of chaetae on last whorl and other whorls have two rows of chaetae. However, *C. menglaensis* and *C. yunnanensis* are small, up to 30 mm, smooth and solid, suggesting that *C. menglaensis* and *C. yunnanensis* belong to the genus *Mekongia*. It is also possible that *C. dianchiensis* could belong to the genus *Margarya* due to several characteristics: shell thick with ridges, female pouch with few big embryos and embryos shell with ridges (not chaetae). Similarly, *Cipangopaludina ampullacea* and *C. lecythis*, *C. fluminalis* and *C. chinensis* can be distinguished by shell characteristics, but they do not appear to possess any obviously distinctive anatomy, placing *C. ampullacea* and *C. fluminalis* as a subspecies of *C. lecythis* and *C. chinensis*, respectively. Our analysis also placed *C. leucostoma* (Heude) and *C. diminuta* (Heude) as synonymous with *C. patris* (Kobelt) according to apex obtuse and less than 6 whorls. However, according to the International Code of Zoological Nomenclature (ICZN, 1999), *C. leucostoma* should be valid due to its publication earlier than *C. patris*. Finally, *Cipangopaludina wingatei* and *C. ampulliformis* were found to be synonyms of *C. chinensis* and *C. lecythis*, respectively.

Totally, our analysis of 18 *Cipangopaludina* species resulted in a revised taxonomy that includes 11 species and 2 subspecies recorded in China, viz. *C. aubryana*, *C. cathayensis*, *C. chinensis*, *C. haasi*, *C. hainanensis*, *C. latissima*, *C. lecythis*, *C. lecythoides*, *C. leucostoma*, *C. ussuriensis*, *C. ventricosa* and *C. chinensis fluminalis*, *C. lecythis ampullacea*. Based on whether or not the spiral whorl depth was longer than aperture depth, Chinese

Cipangopaludina species could be divided to two groups, the *chinensis* group with spiral whorl depth longer than aperture depth that includes *C. chinensis*, *C. haasi*, *C. ussuriensis* and *C. c. fluminalis*, and the other the *cathayensis* group with spiral whorl depth being shorter than aperture depth, including *C. aubryana*, *C. cathayensis*, *C. hainanensis*, *C. latissima*, *C. lecythis*, *C. lecythoides*, *C. leucostoma*, *C. ventricosa* and *C. l. ampullacea*. Several anatomical characteristics can also help distinguish between the two groups. For example, the *chinensis* group can be distinguished from *cathayensis* group by vas deferens: *chinensis* group species with more than 5 (*C. haasi* with 8) parallel secondary branches in anterior branch, while *cathayensis* group species always with 4 secondary branches. The number of secondary branches of vas deferens are in connection with size of body whorl. The shell of *chinensis* group species was taller, with body whorl depth being the same or longer than body width, making the vas deferens longer and with more secondary branches, especially in *C. haasi*. However, the body whorl of *cathayensis* group species is inflated, with body whorl depth shorter than body width, resulting in vas deferens being short and fat, and the secondary branch with many tiny branches, looking rather similar to a lush tree.

Within each group, there are further defining characteristics of individual species. In *chinensis* group, *C. ussuriensis* can be easily distinguished from other species by body whorl with 4 ridges and colour band. *Cipangopaludina haasi* can be distinguished from other species by body whorl not inflated, vas deferens with 8 secondary branches in anterior branch and vas deferens opens in last 1/4 of testis. *Cipangopaludina chinensis fluminalis*, however, is quite similar with *C. chinensis*, except for the shell thick vs. thin; umbilicus big and deeply vs. small or closed. In *cathayensis* group, *C. latissima* could be distinguished from other species by its markedly enlarged aperture while *C. hainanensis* can be distinguished from other species by apex eroded, left 4 whorls. According to kidney shape, the other species could be divided to two subgroups. Triple shape, including *C. cathayensis*, *C. aubryana* and *C. lecythis*, and arch shape, including *C. l. ampullacea*, *C. leucostoma* and *C. ventricosa*. *Cipangopaludina lecythis* can be distinguished from *C. cathayensis* and *C. aubryana* by vas deferens with 2 branches and opens in last 1/4 of testis vs. 3 branches and 1/3, and *C. cathayensis* can be distinguished from *C. aubryana* by the

anterior 2/3 part of osphradium ridge-like and posterior 1/3 part inflated. *Cipangopaludina leucostoma* can be distinguished from *C. l. ampullacea* and *C. ventricosa* by vas deferens opening in last 1/3 vs. 1/4, and *C. ventricosa* can be distinguished from *C. l. ampullacea* by vas deferens with 3 branches vs. 2 branches.

Similar to our study, most viviparids are primarily delineated by their shells, though a few observations on the anatomy have also been made. Vail (1977) for example mentioned that the reproductive system was a useful characteristics to delineate viviparid subfamilies and genera by anatomical studies of mature male and female *Campeloma geniculum* (Conrad, 1834), *Lioplax pilsbryi* Walker, 1905 and *Viviparus georgianus* (Lea, 1834). Simone (2004) and Rao (1925) also reported intergeneric differences in the central nervous system, stomach lining and form of the ctenidial filaments in the five Asian genera. Du et al (2011) later reported a difference in kidney shape and the number of embryos present in the uterus of four Chinese viviparids, *Angulygra*, *Cipangopaludina*, *Margarya* and *Trochotaia*. In this study, the size of osphradium, location of vas deferens opens and the number of secondary branches, kidney shape were useful anatomical characteristics to identify interspecies of *Cipangopaludina*. The allometric growth or environmental effects could result in intraspecific variations in shell morphology and operculum (Chiu et al, 2002), but these anatomical characteristics could be used to identify young specimen.

Given the difficulties in identifying species solely by shell characters, further description of such species anatomical characteristics of both young and mature individuals may prove useful in further refining the taxonomy and identifying species and determining their validity. Unfortunately, until further studies are undertaken that more accurately characterize the anatomy or even underlying genetic differences, there will remain a variety of unanswered or unanswerable questions. To date, the monophyly of *Cipangopaludina* is still unresolved. A recent study by Du et al (2013) on the phylogeny of *Margarya* based on combined CO I and 16S rRNA sequences indicated that *Cipangopaludina* is not a monophyly, since species cluster with *Margarya*; however, the specimens of *Cipangopaludina* and *Margarya* are from Lake Dianchi. Likely further studies into the phylogeny and ecology of the *Cipangopaludina* in different environments and distributions will further enhance our understanding of these organisms.

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