

Molecular phylogeny and morphological evolution of the Chinese land snail *Cathaica* Möllendorff, 1884 (Eupulmonata: Camaenidae) in Shandong Province, China

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Cathaica is a genus of bradybaenid land snails occurring in China and is widespread in Shandong Province. Here we re-describe three species, *C. pyrroazona*, *C. fasciola* and *C. leei*, and describe two new species, *Cathaica fohuiensis* Zhang sp. nov. and *Cathaica multcostata* Zhang sp. nov.. Geometric morphometric analyses demonstrate that *C. pyrroazona*, *C. fasciola*, *C. leei* and *C. fohuiensis* are conchologically similar. Based on differences in their genitalia and molecular data, we consider *C. pyrroazona* and *C. fasciola* to be distinct species. This re-establishes *C. pyrroazona* as the type species of *Cathaica*. *Cathaica leei* can be distinguished based on its plate spiral whorl and wide umbilicus. The new species *C. fohuiensis*, with a conical shell and expanded vaginal base, can be distinguished from other *Cathaica* species based on morphological criteria and is robustly supported in the phylogenetic tree. The other new species, *C. multcostata*, possesses a strongly ribbed discoid shell and exhibits mucous glands that cluster tightly with the vagina. It is robustly supported in the phylogenetic tree and is the sister taxon to the other *Cathaica* species. Based on morphological characters and our molecular tree, *Pliocathaica*, represented here by *P. buwigneri*, *P. pulveratricula* and *P. gansuica*, is not monophyletic.

ADDITIONAL KEYWORDS: Bradybaeninae – *Cathaica* – character mapping – cladistic species concept – molecular phylogeny – *Pliocathaica*.

INTRODUCTION

There are ~70 Chinese species and subspecies in the Bradybaeninae genus *Cathaica* Möllendorff, 1884 (Gredler, 1878, 1882; Tryon, 1887; Moellendorff, 1899; Andrae, 1900; Gude 1902a, 1902b; Yen, 1935, 1939; Zilch, 1960, 1968; Chen & Zhang, 2004). *Pseudiberus* Ancy, 1887 was included as a subgenus in *Cathaica* by Andrae (1900). However, it has been treated as distinct from *Cathaica* by some authors (Pilsbry, 1894; Möllendorff, 1899; Richardson, 1983; Zhang et al. 2020). In addition, Andrae (1900) described four additional subgenera in *Cathaica*, namely *Eucathaica* (= *Cathaica*), *Pliocathaica*, *Xerocathaica* and *Campylocathaica*. Gude (1902a) followed Andrae (1900). These four subgenera were subsequently subsumed into the *Cathaica* subgenus as sections by Thiele (1931). Subsequently, they were again raised as

subgenera by Zilch (1960). Richardson (1983) largely followed Andrae (1900), but treated *Pseudiberus* as a distinct genus. Chen & Zhang (2004) followed the taxonomy of Richardson (1983) and Schileyko (2004) largely followed Richardson (1983), except for treating *Campylocathaica* as a synonym of *Fruticicola*. The subgenus level has sometimes been raised to the genus level in classifications. For example, Wu (2004, 2019) raised *Pliocathaica* as a genus (Table 1). Occasionally, the subgenus *Cathaica* has been treated without subdivision (e.g. Yen, 1939). Here, we provisionally treat *Cathaica*, *Pliocathaica* and *Pseudiberus* as separate genera following Wu (2004, 2019) with the subgenera *Cathaica*, *Xerocathaica* and *Campylocathaica* retained within *Cathaica* following Andrae (1900), Richardson (1983) and Chen & Zhang (2004) (see Table 1). *Cathaica sensu stricto* (s.s.) is used here to refer to the subgenus *Cathaica* (Table 1).

Nearly all species of *Cathaica* and related genera have been described solely on the basis of their

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Table 1. Historical taxonomy of *Cathaica* subgenera in [Andreae \(1900\)](#). Subgenera are given in parentheses.

Andreae (1900), Gude (1902a)	Thiele (1931)	Zilch (1960)
<i>Cathaica</i> (<i>Eucathaica</i>)	<i>Cathaica</i> (<i>Cathaica</i>) section <i>Cathaica</i>	<i>Cathaica</i> (<i>Cathaica</i> s.s.)
<i>Cathaica</i> (<i>Pliocathaica</i>)	<i>Cathaica</i> (<i>Cathaica</i>) section <i>Pliocathaica</i>	<i>Cathaica</i> (<i>Pliocathaica</i>)
<i>Cathaica</i> (<i>Xerocathaica</i>)	<i>Cathaica</i> (<i>Cathaica</i>) section <i>Xerocathaica</i>	<i>Cathaica</i> (<i>Xerocathaica</i>)
<i>Cathaica</i> (<i>Campylocathaica</i>)	<i>Cathaica</i> (<i>Cathaica</i>) section <i>Campylocathaica</i>	<i>Cathaica</i> (<i>Campylocathaica</i>)
<i>Cathaica</i> (<i>Pseudiberus</i>)	<i>Cathaica</i> (<i>Cathaica</i>) section <i>Kaznakoviella</i>	<i>Cathaica</i> (<i>Kaznakoviella</i>)
	<i>Cathaica</i> (<i>Pseudiberus</i>) section <i>Pseudiberus</i>	<i>Pseudiberus</i> (<i>Pseudiberus</i>)
	<i>Cathaica</i> (<i>Pseudiberus</i>) section <i>Platypetasus</i>	<i>Pseudiberus</i> (<i>Platypetasus</i>)
Richardson (1983)	Schileyko (2004)	Chen & Zhang (2004)
<i>Cathaica</i> (<i>Eucathaica</i>)	<i>Cathaica</i> (<i>Cathaica</i> s.s.)	<i>Cathaica</i> (<i>Cathaica</i>)
<i>Cathaica</i> (<i>Pliocathaica</i>)	<i>Cathaica</i> (<i>Pliocathaica</i>)	<i>Cathaica</i> (<i>Pliocathaica</i>)
<i>Cathaica</i> (<i>Xerocathaica</i>)	<i>Cathaica</i> (<i>Xerocathaica</i>)	<i>Cathaica</i> (<i>Xerocathaica</i>)
<i>Cathaica</i> (<i>Campylocathaica</i>)	<i>Fruticicola</i>	<i>Cathaica</i> (<i>Campylocathaica</i>)
<i>Pseudiberus</i>	<i>Pseudiberus</i>	<i>Pseudiberus</i> (<i>Pseudiberus</i>)
	<i>Platypetasus</i>	<i>Pseudiberus</i> (<i>Platypetasus</i>)
Wu (2004, 2019)	This study	
<i>Cathaica</i>	<i>Cathaica</i> (<i>Cathaica</i>) [= <i>Cathaica</i> s.s.]	
<i>Pliocathaica</i>	<i>Cathaica</i> (<i>Xerocathaica</i>)	
<i>Pseudiberus</i>	<i>Cathaica</i> (<i>Campylocathaica</i>)	
	<i>Pliocathaica</i>	
	<i>Pseudiberus</i>	

shell characters. The main conchological features emphasized in previous taxonomic treatments were shell form (ranging from globular to discoid) and the presence or absence of an apertural tooth. In material identified as *C. pyrrhizona*, the type species of *Cathaica*, the shell is somewhat depressed with several brown spiral bands on the body whorl. The genital system encompasses a dart sac and accessory dart sac, a complex of branched mucous glands, and a penis with a penial sheath ([Tryon, 1887](#); [Schileyko, 2004](#); [Wu, 2004](#)).

The distribution of different subgenera of *Cathaica* varies considerably. Species within *Cathaica* s.s. mainly inhabit the Chinese provinces of Shandong, Henan and Hebei ([Deshayes, 1874](#), [Hilber von, 1882](#), [Ping, 1929](#), [Yen, 1939](#), [Chen & Zhang, 1987](#)). Within this region, the Taihang mountain chain, the Yimeng mountains and Mount Tai represent significant habitats. About 55 species are currently included in *Cathaica* s.s. Two common members, *Cathaica pyrrhizona* (Philippi, 1847) and *C. fasciola* (Draparnaud, 1801), are widely distributed in Southern China. The subgenera *Xerocathaica* and *Campylocathaica* contain only a few species inhabiting Western China, with 11 species attributed to *Xerocathaica* and four attributed to *Campylocathaica* ([Andreae, 1900](#); [Thiele, 1931](#)). Overall, species of the genus *Cathaica* inhabit arid or semi-arid regions, including Shandong and other provinces mostly north of the Yangtze River.

On the basis of the phylogenetic tree generated by [Wu \(2004\)](#) based on genital characters, *Cathaica*

clusters with *Pseudiberus*, *Pseudobuliminus* and *Metodontia*, and is the sister group of *Bradybaena* and *Trichobrybaena*. According to [Wu \(2004, 2019\)](#), *Pliocathaica* is the sister group of *Karafkaohelix*. *Cathaica* can be distinguished from other Bradybaeninae by the presence of an accessory sac, the presence of a 'poly-layer structure' in the accessory sac, and the lack of flagellum and penial caecum.

Herein, we use comparative shell morphology and anatomy and employ molecular phylogenetics to investigate the systematic relationships of *Cathaica* and other related species within Shandong Province.

MATERIALS AND METHODS

BIOLOGICAL MATERIAL

Cathaica specimens were collected from Shandong Province, China, between 2017 and 2021, with collections focused on Mount Tai and adjacent regions and in the Yimeng Mountains Chain ([Fig. 1](#); [Supporting Information, Table S1](#)). All specimens of *Cathaica* obtained in this study, *Cathaica fasciola*, *C. pyrrhizona*, *C. leei*, *C. fohuiensis*, *C. multicostata*, *C. sp1* and *C. sp2*, were from the subgenus *Cathaica* (*Cathaica* s.s.). Specimens of *C. sp1* and *C. sp2* were distinguished as distinct from other *Cathaica* species but not identified to species and consequently named *C. sp1* and *C. sp2*. Additionally, *Pliocathaica pulveratricula*, *Pliocathaica buvigneri*, *Pliocathaica gansuica* and *Pseudiberus* specimens were obtained

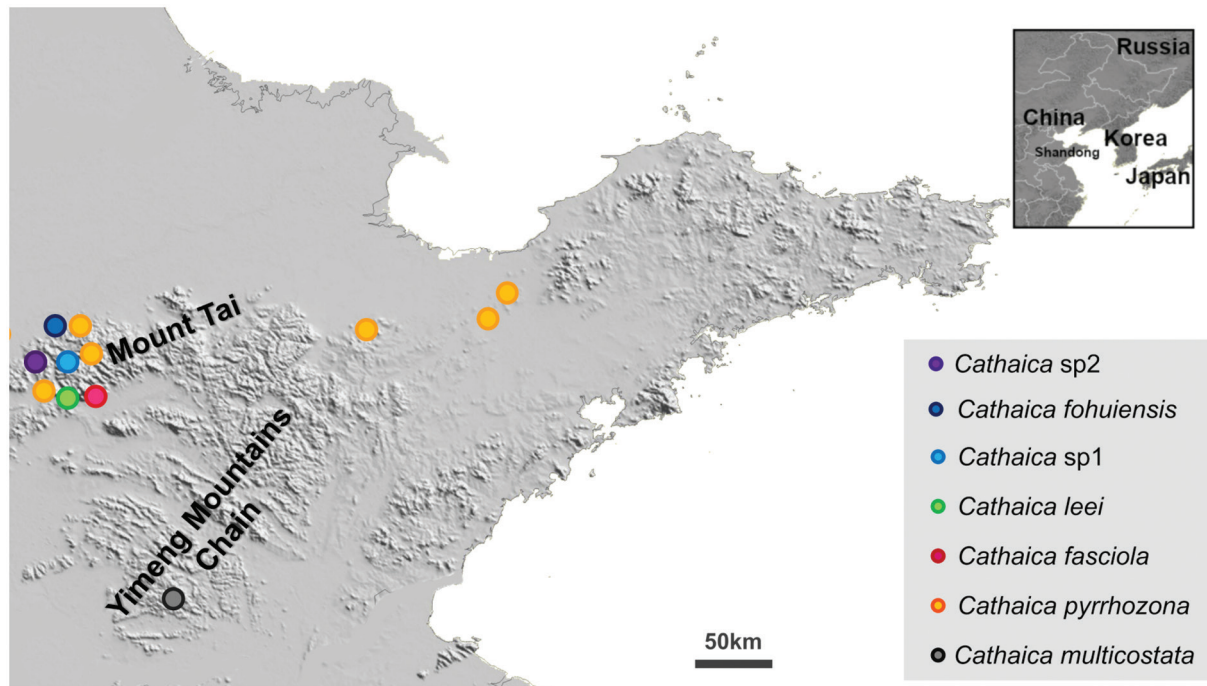


Figure 1. Sample collection sites of *Cathaica s.s.* species in Shandong Province, China.

from Shandong, Anhui, Henan, Hebei, Shaaxi and Gansu Provinces (Supporting Information, Table S1). Live adult snails were relaxed in 5% ethanol for 6 h prior to preservation in 75% ethanol and the ethanol was changed regularly when the specimens were fresh to keep the concentration at 75%. Additionally, shells of *Pliocathaica subrugosa* in museums were checked.

MORPHOLOGICAL ANALYSIS

Photographs of shells and genitalia were taken with a camera (Canon EOS 650D) or a stereo microscope (Leica S6D). The shell and genitalia were measured to the nearest 0.1 mm with digital vernier calipers. The whorl number was recorded with 0.125 whorl accuracy as described by Kerney & Cameron (1979). Soft parts were measured after the specimens were fixed in 75% ethanol.

Directions used in descriptions of genitalia are as follows: proximal = towards the genital atrium; distal = away from the genital atrium; left = on the left side of the plane formed by both the dart sac and the vagina that opens upward; right = on the right side of the plane formed by both the dart sac and the vagina that opens upward.

Shell morphological variation was measured using the tps series software including tpsUtil (Rohlf, 2004a) and tpsDig (Rohlf, 2004b), using the geometric morphometrics (GM) method. From an apertural view of the shell, landmarks (points directly based on

the topography of the aperture) and semi-landmarks (algebraic transformations derived from the homological curve of the aperture) were recorded. The location of the landmarks and semi-landmarks are as follows: LM1, the columella insertion; LM2, the right terminal point at the carina on the penultimate whorl; LM3, the right terminal point at the carina on the whorl before the penultimate whorl; LM4, apex (embryonic shell); LM5, the left terminal point at the carina on the whorl before the penultimate whorl; LM6, the left terminal point at the carina on the body whorl; LM7, the intersection of the peristome and contour of the body whorl; LM8, the end of the carina on the body whorl/peristome; LMs 9–36, semi-landmarks on the outline between LM6 and LM7 by length; and LMs 37–72, semi-landmarks on the contour of the aperture by length, from LM1 via LM8 to LM2 (Fig. 2). The landmarks and semi-landmarks were treated indiscriminately. A total of 89 shells were included in the GM analyses. Principal coordinates analysis (PCA) and canonical variate analysis (CVA) were performed using MorphoJ 1.07a (Klingenberg, 2011) for *C. pyrrhozona*, *C. fasciola*, *C. leei* and *C. fohuiensis* to determine if there were any significant conchological differences among them. *Cathaica multicosata* was excluded from these analyses owing to its unique shell shape. Likewise, materials of *C. sp1* and *C. sp2* were limited and therefore these specimens were also excluded from the analyses. PCAs and CVAs were not undertaken for *Pliocathaica* members as *Pliocathaica* species can be readily distinguished by their shells.

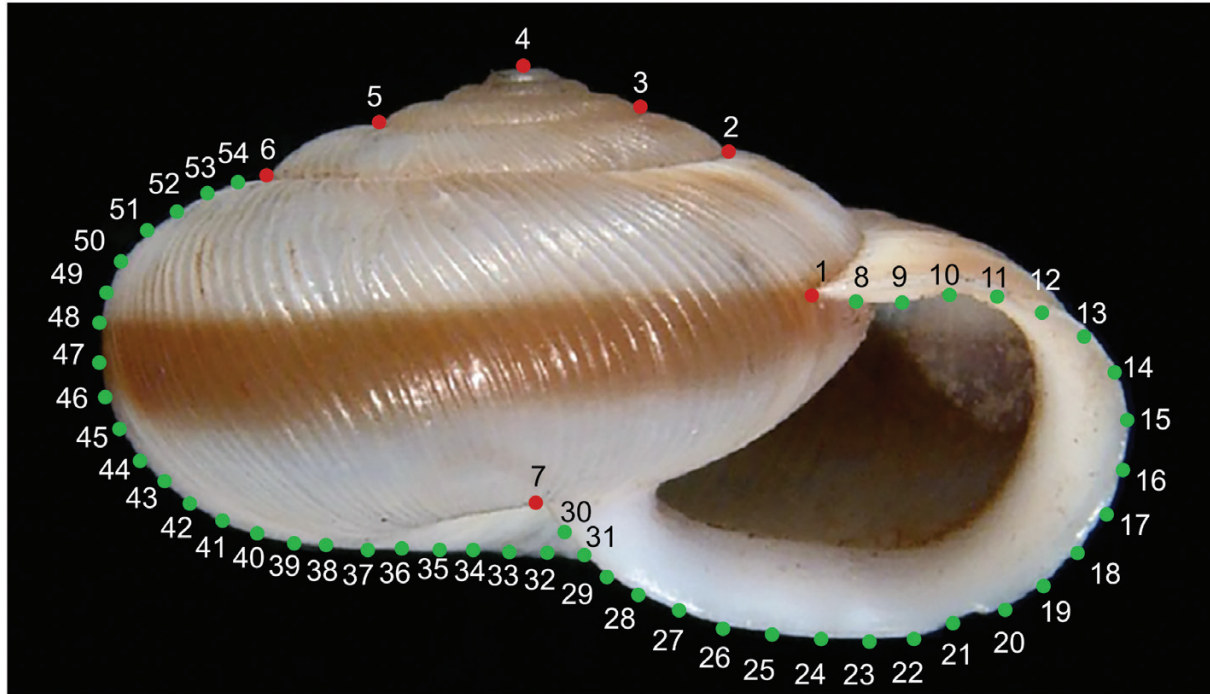


Figure 2. Landmarks for morphometric geometric analyses. Red dot, landmark; green dot, semi-landmark.

DNA EXTRACTION, PCR AND SEQUENCING

Whole DNA was extracted from a 1-mm³ piece of pedal muscle using either the Tiangen DP316 kit following the manufacturer's instructions or CTAB method (Goodacre & Wade, 2001). An ~450-bp section of the mitochondrial 16S rRNA gene and an ~750-bp section of the internal transcribed spacer 2 (ITS2) region were amplified using polymerase chain reaction (PCR). Each 25- μ L PCR mix consisted of 12.5 μ L cwbio 2 \times Es Taq MasterMix Dye or Bionline Taq MasterMix, 9.5 μ L ddH₂O, 1 μ L 10 μ M forward primer, 1 μ L 10 μ M reverse primer and 1 μ L template DNA. For 16S, we used the 16Sar (forward, CGCCTGTTTATCAAAAACAT) and 16Sbr (reverse, CCGGTCTGAACTCAGATCACGT) primers and the conditions for thermal cycling were 30 s at 94 °C for pre-denaturing followed by 40 cycles of 10 s at 94 °C, 50 s at 45 °C and 50 s at 72 °C, and a final extension at 72 °C for 10 min. For ITS2, we used the 18d (forward, CACACCGCCCGTCGCTACTACCGATTG) and ITS-4 (reverse, TCCTCCGCTTATTGATATGC) primers and the reaction conditions were 2 min at 94 °C for pre-denaturing, 30 cycles of 30 s at 94 °C, 30 s at 50 °C and 90 s at 72 °C, and a final extension at 72 °C for 2 min. The amplicons were examined on a 1% agarose gel for quality and fragment size and sequenced on an automated sequencer by sequencing companies Tsingke and Macrogen.

SEQUENCE ANALYSIS

Chromatographs were examined and sequences compiled in SeqMan 7 (Swindell & Plasterer, 1997). Sequence alignment was performed by MAFFT 7.490 (Nakamura *et al.*, 2018) with alignments trimmed using Gblocks 0.91b (Castresana, 2000). The 16S and ITS2 alignments were concatenated using SequenceMatrix 1.9 (Vaidya *et al.*, 2011). The p-distances among and within species groups (as defined by morphological characteristics) were calculated using MEGA 11 (Tamura *et al.*, 2021). Sequence evolution models were selected for the datasets using ModelTest-NG 0.1.7. (Darriba *et al.*, 2020), with the GTR+G and HKY+G models selected as the best nucleotide substitution models for 16S and ITS2 respectively.

A combined matrix of 661-bp sites for 42 samples was used for the subsequent phylogenetic analyses. Bayesian inference (BI) phylogenies were generated using MrBayes 3.2.7 (Ronquist *et al.*, 2012) with two runs for 4 000 000 generations sampling every 2000 generations and a temperature of 0.07. The final tree and posterior probabilities were determined based on the last 50% of trees (burnin = 0.5). Maximum-likelihood (ML) phylogenetic trees were generated using RAxML-NG 1.1.0 (Kozlov *et al.*, 2019) using a heuristic search strategy with ten random plus ten parsimony start trees and subtree pruning and

regrafting (SPR) branch swapping. Bootstrap analysis was undertaken for the ML tree with 1000 bootstrap replicates. Maximum-parsimony (MP) phylogenetic trees were generated using TNT 1.5 (Goloboff & Catalano, 2016). MP analysis was performed with implied weighting with the weighting set as 12 according to recommendations (Goloboff *et al.*, 2017) and tree searching with tree bisection reconnection (TBR). Bootstrap analysis was undertaken for MP with 1000 replicates, and the consistency index (CI) and retention index (RI) were calculated using the stats.run script provided by TNT. The specimens used in phylogenetic analysis are listed in [Supporting Information, Table S2](#).

CHARACTER MAPPING

Morphological characteristics were mapped onto the generated phylogenetic trees using WinClada 2.0 (Nixon, 2021). Morphological characters were obtained from this study and from Wu (2004, 2019). Morphological characters were scored and written in TNT format (Goloboff, 2022); see [Supporting Information, File S1](#) for details of morphological characters. The character scoring standard is listed below.

char0: Proximal accessory sac (0) single, (1) double, (2) absent; **char1:** Single proximal accessory sac on which side of dart sac (0) right, (1) left; **char2:** Entrance of proximal accessory sac leads to (0) dart sac chamber, (1) dart chamber, (2) atrium; **char3:** Entrance of mucous glands leads to (0) dart sac chamber, (1) dart chamber, (2) accessory sac chamber; **char4:** Mucous glands (0) not tight, (1) tight; **char5:** Vagina open to (0) dart chamber, (1) atrium; **char6:** Vagina basal (0) not expanded, (1) expanded; **char7:** Penial pilasters (0) cross interlocked, (1) parallel; **char8:** Epiphallial papilla (0) absent, (1) present; **char9:** Poly-layered structure (0) absent, (1) present; **char10:** Distal vagina membranous near atrium (0) absent, (1) present; **char11:** Accessory sac (0) absent, (1) present.

TAXONOMIC-LEVEL DELIMITATION ANALYSIS

Taxonomic-level delimitation tests were performed using ASAP (Puillandre *et al.*, 2020) and mPTP 0.2.4 (Kaplí *et al.*, 2017). For ASAP analysis, p-distances calculated by MEGA 11 were used. For mPTP analysis, BI trees based on 16S and ITS2 separately were used, with the two trees generated by MrBayes following the methods described above. Both ML and Markov chain Monte Carlo (MCMC) mPTP analyses following the PTP model (Zhang *et al.*, 2013) were performed with default settings.

We use the cladistic species concept for species definition, which defines species as a monophyletic group based on homologous characters and includes both biological and ecological characters (Ridley, 1989).

Abbreviations used here are: a.s.l., above sea level; At, atrium; BC, bursa copulatrix; BCD, bursa copulatrix duct; NHM, Natural History Museum, London; NHMUK, when citing NHM registration numbers; DS, dart sac; DSC, dart sac chamber, the internal space incompletely closed by distal dart sac and SD (see below); Dt, love dart; DtC, love dart chamber; DVM, membranous sac surrounding distal region of vagina near atrium; FMA, fully mature animal(s); FO, free oviduct; GZ, Guoyi Zhang; HBUMM, mollusc collection of Museum of Hebei University, Hebei, China; MG, mucous glands; MGE, entrance(s) of mucous glands; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; P, penis; PAS, proximal accessory sac, a blind sac on proximal dart sac and opening into dart sac chamber or not; PASE, entrance of proximal accessory sac; PLs, poly-layered structures; PR, penial retractor muscle; PS, penis sheath; SD, septum between atrial opening and opening of DtC; SDNU, the Zoological Collection, Shandong Normal University, Jinan, China; SDP, Shandong Province, China; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany; spec, specimen; THZ, Tianjin Hoang-Paiho Zoological Collection, Tianjin City, China; Va, vagina; VD, vas deferens.

RESULTS

We examined 110 specimens of five *Cathaica s.s.* species mostly from Shandong Province, but with some samples from Anhui Province and Gansu Province. Additionally, we examined 166 specimens of *Pliocathaica* from Shandong, Anhui, Henan, Hebei, Shanxi and Gansu Provinces, China.

MORPHOLOGICAL ANALYSIS

Examination of the shell (Fig. 3) showed that *C. fasciola* and *C. pyrroazona* could not be distinguished with statistical significance (Fig. 3A–C). *Cathaica leei* is distinguished by a low spired shell with wide umbilicus (Fig. 3D). *Cathaica multicostata* is also discoid but can be distinguished from *C. leei* by having strong ribs (Fig. 3E). *Cathaica fohuiensis* can be recognized from its conical shell (Fig. 3F).

Four arrangements can be recognized in the genital system of *Cathaica* (Fig. 4A–D). (1) two proximal accessory sacs on the right and left sides of the dart sac, vagina open to atrium and unexpanded, entrance(s) of mucous glands leading to dart sac chamber, and mucous glands proximally attached to the vagina (not

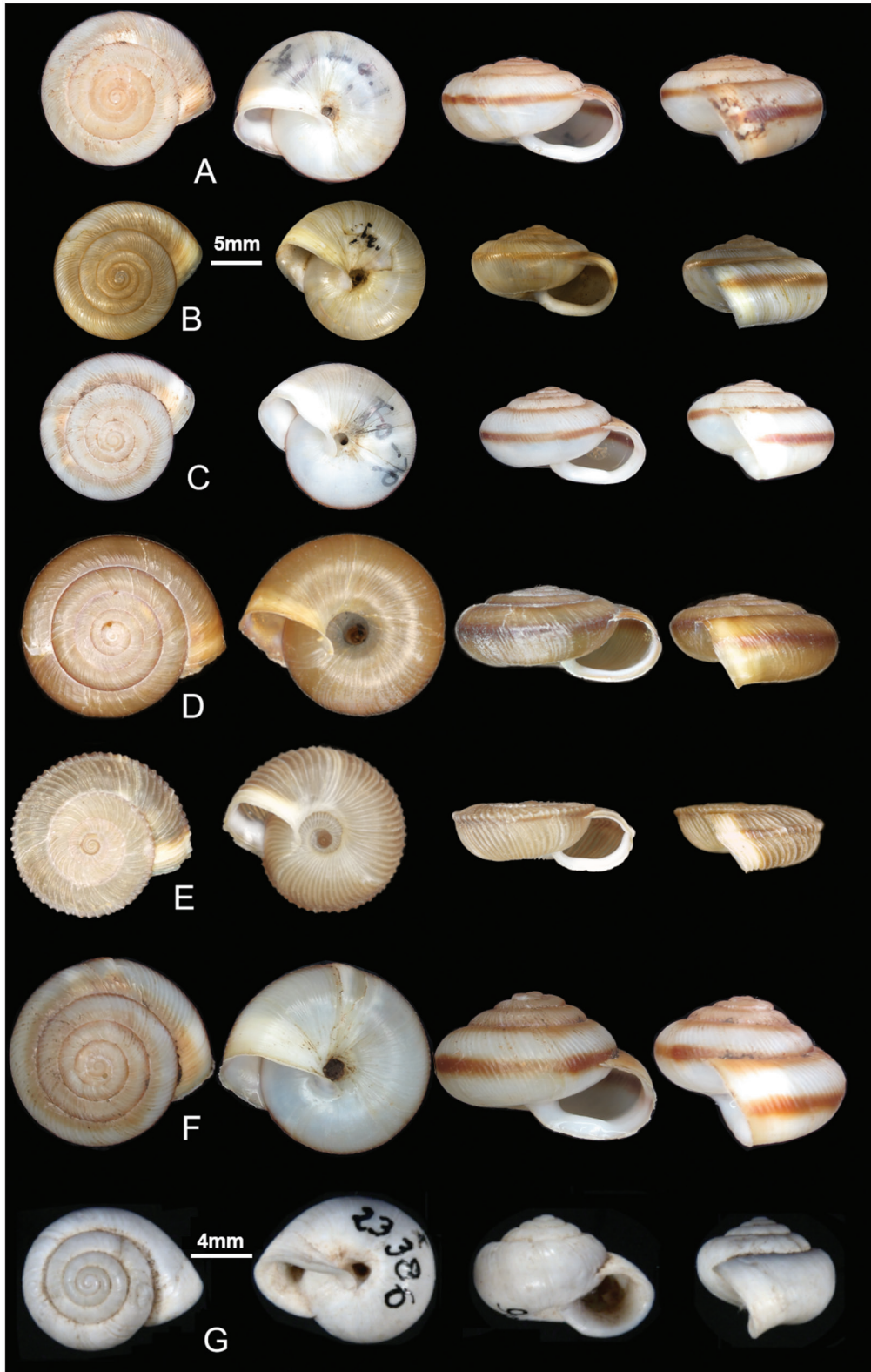


Figure 3. Four views of *Cathaica* and *Pliocathaica* shells from Shandong: A, *Cathaica fasciola*; B, *C. fasciola*, holotype; C, *C. pyrroazona*; D, *C. lei*; E, *C. multicostata* sp. nov.; F, *C. fohuiensis* sp. nov.; G, *Pliocathaica buvigneri*. The scale bar of 5 mm is for *Cathaica* species (A–G), whereas the scale bar of 4 mm is for *Pliocathaica* species (F).

tightly) before entering the dart sac. *Cathaica fasciola* Draparnaud, 1801 has this arrangement (Fig. 4A). (2) Proximal accessory sac on the right side of the dart sac, vagina open to atrium and unexpanded, entrance(s) of mucous glands leading to dart sac chamber, and mucous glands proximally attached to the vagina (not tightly) before entering the dart sac. *Cathaica pyrroazona* Philippi, 1847 and *C. leei* Yen, 1935 have this arrangement (Fig. 4B). (3) Proximal accessory sac on the right side of the dart sac, vagina open to atrium and expanded, entrance(s) of mucous glands leading to the dart sac chamber, and mucous glands proximally attached to vagina tightly before entering the dart sac. *Cathaica fohuiensis* Zhang, sp. nov. has this arrangement (Fig. 4C). (4) Proximal accessory sac on the right side of the dart sac, vagina open to atrium and unexpanded, entrance(s) of mucous glands leading to dart sac chamber, and mucous glands proximally attached to vagina tightly before entering dart sac. *Cathaica multicostata* Zhang, sp. nov. has this arrangement (Fig. 4D).

Each *Cathaica s.s.* species has distinct morphological characters of the genital system or shells. *Cathaica fasciola* has two proximal accessory sacs, one on each side of the dart sac (Fig. 4A). *Cathaica fohuiensis* sp. nov., *C. multicostata* sp. nov., *C. leei* and *C. pyrroazona* each have a single proximal accessory sac on the right side of the dart sac (Fig. 4B–D). In *C. fohuiensis* sp. nov., the base of the vagina is enlarged when compared to *C. pyrroazona* and *C. leei* (Fig. 4C). *Cathaica multicostata* is significantly different from other *Cathaica s.s.* species because of its strong ribs and distinctively flat apex; its genital system (Fig. 4D) differs in the position of the mucous glands, which enter the dart sac immediately proximal to the vagina; and the position at which the vagina enters into the dart sac is lower than in other *Cathaica s.s.* species from Shandong.

In species attributed to *Pliocathaica*, two arrangements of the genital system can be recognized (Fig. 4E–F). (1) Proximal accessory sac on the left side of the dart sac, vagina open to the dart sac chamber and unexpanded, entrance(s) of mucous glands leading to dart chamber, and mucous glands proximally attached to the vagina tightly before entering the dart sac. *Pliocathaica buvigneri* Deshayes, 1873 has this arrangement (Fig. 4E). (2) Proximal accessory sac on the left side of the dart sac, vagina open to atrium and unexpanded, entrance(s) of mucous glands leading to atrium, and mucous glands proximally attached to vagina tightly before entering the dart sac. *Pliocathaica pulveratricula* Martens, 1882 has this arrangement (Fig. 4E).

Species that have been attributed to *Pliocathaica* have distinct morphological characters. The location of the vaginal entrance in *Pliocathaica buvigneri* (Fig. 4E) is similar to that in *C. multicostata*, but the

mucous glands enter into the dart chamber instead of the dart sac chamber as they do in *Cathaica s.s.* In *Cathaica s.s.* the proximal accessory sac is on the right side of the dart sac except in *C. fasciola*, where the proximal accessory sac is double, on both the left and the right. The studied *Pliocathaica* always have the proximal accessory sac on the left side of the dart sac, except *Pliocathaica gansuica* which does not have a proximal accessory sac. *Pliocathaica buvigneri* is also distinguished by a thicker shell and a gradually expanded aperture (Fig. 3G). In *Pliocathaica pulveratricula* (Fig. 4F) the mucous glands enter the atrium instead of the dart sac chamber and dart chamber. The direction of the proximal accessory sac is the same as in *Pliocathaica buvigneri*.

The shells of species attributed to *Pliocathaica* in this study can be readily distinguished by visual inspection of their shells and PCAs and CVAs were unnecessary and not undertaken.

In the scatter plots of PCA scores based on landmarks and semi-landmarks from apertural views of *Cathaica s.s.* species from Shandong, PC1 explains 36.925% and PC2 explains 31.319% of the total shape variation of shells (Fig. 5A). *Cathaica pyrroazona* exhibits significant variation and cannot be distinguished from the other *Cathaica s.s.* species included in the PCA. Indeed, there is no clear separation between any of the species in the PCA.

In the scatter plots of CVA scores based on landmarks and semi-landmarks from apertural views of *Cathaica s.s.* species from Shandong, CV1 explains 72.192% and CV2 explains 20.4% of the total shape variation of shells (Fig. 5B). CVA has been undertaken based on group data with individuals preliminarily assigned to groups based on the genital system, which was used as the grouping standard. Here *C. fasciola*, *C. pyrroazona* and *C. leei* formed clearly individualized clusters. However, *C. fohuiensis* did not and clustered with either *C. fasciola* or *C. pyrroazona*.

MOLECULAR PHYLOGENETIC ANALYSES

The phylogenetic tree of species attributed to *Cathaica* and *Pliocathaica* from Shandong based on Bayesian inference is shown in Figure 6. *Camaena cicatricosa* was used as the outgroup to root the phylogenetic tree and the tree also includes *Pseudiberus*, *Euhadra* and *Bradybaena*. The BI, ML and MP trees had highly consistent topologies. *Cathaica s.s.* is monophyletic with representatives of *Cathaica s.s.* clustering together in the tree with relatively strong support [posterior probability (PP) = 1.00 BI, 64% ML and 99% MP bootstrap support]. However, *Pliocathaica* is not monophyletic with representatives of the subgenus *Pliocathaica* falling separately between other genera, such as *Pseudiberus* and *Euhadra*. Two main nodes

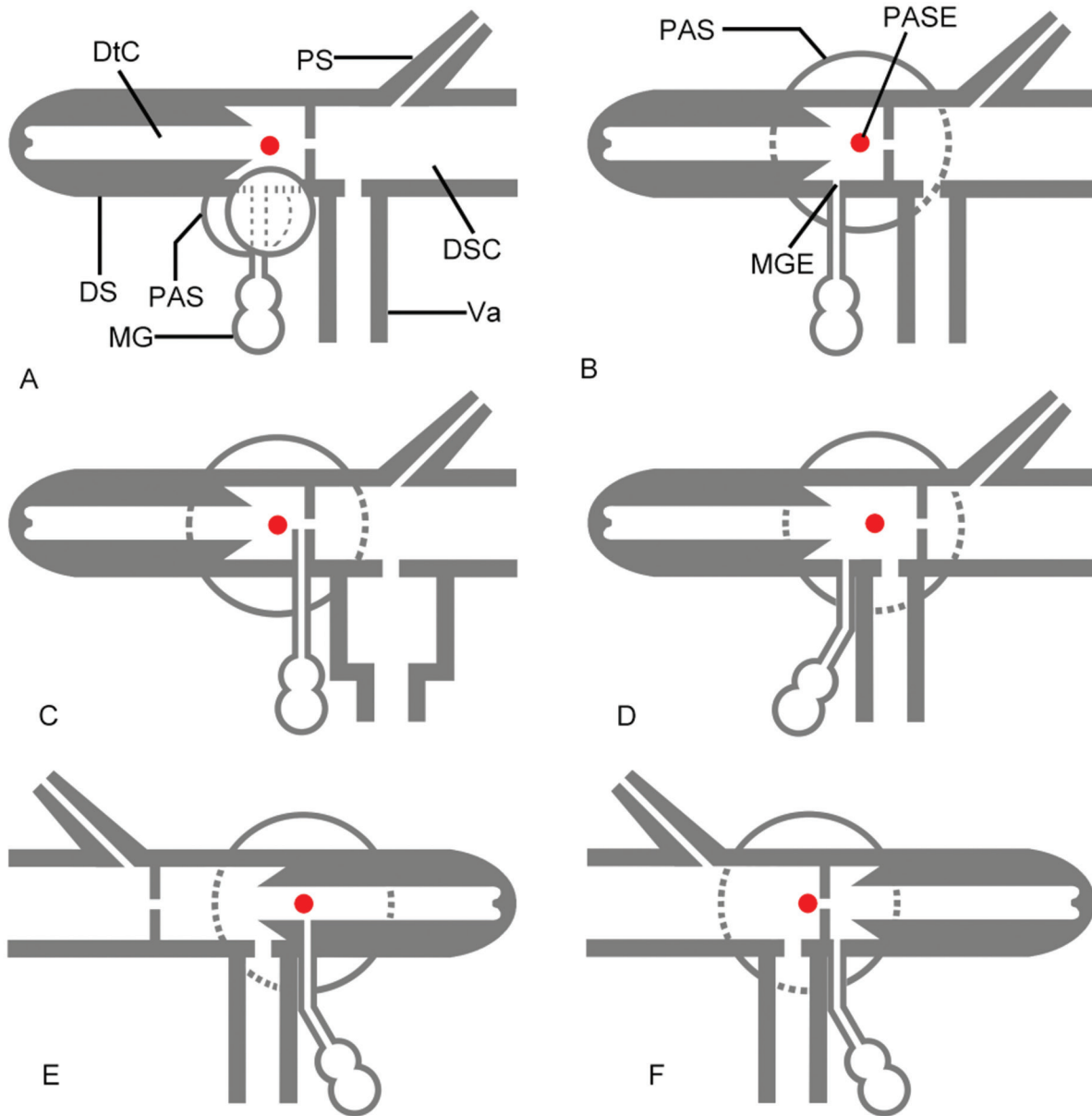


Figure 4. Diagrams of the genitalia. A, two proximal accessory sacs on right and left sides of the dart sac, vagina open to atrium and unexpanded, entrance(s) of mucous glands lead to dart sac chamber, mucous glands proximally attached to vagina not tightly before entering dart sac, such as in *C. fasciola* Draparnaud, 1801; B, proximal accessory sac on right side of dart sac, vagina open to atrium and unexpanded, entrance(s) of mucous glands lead to dart sac chamber, mucous glands proximally attached to vagina not tightly before entering dart sac, such as in *C. pyrrozona* (Philippi, 1847) and *C. lei* Yen, 1935; C, proximal accessory sac on right side of dart sac, vagina open to atrium and expanded, entrance(s) of mucous glands lead to dart sac chamber, mucous glands proximally attached to vagina tightly before entering dart sac, such as in *C. fohuiensis* Zhang *sp. nov.*; D, proximal accessory sac on right side of dart sac, vagina open to atrium and unexpanded, entrance(s) of mucous glands lead to dart sac chamber, mucous glands proximally attached to vagina tightly before entering dart sac, such as in *C. multcostata* Zhang *sp. nov.*; E, proximal accessory sac on left side of dart sac, vagina open to dart sac chamber and unexpanded, entrance(s) of mucous glands lead to dart chamber, mucous glands proximally attached to vagina tightly before entering dart sac, such as in *Pliocathaica buvigneri* (Deshayes, 1873); F, proximal accessory sac on left side of dart sac, vagina open to atrium and unexpanded, entrance(s) of mucous glands lead to atrium, mucous glands proximally attached to vagina tightly before entering dart sac, such as in *P. pulveratricula* (Martens, 1882).

are robustly supported in the tree, one is *Cathaica s.s.* plus *Pliocathaica buwigneri* (PP = 1.00 BI, 85% ML and 69% MP bootstrap support), the other is *Pliocathaica pulveratricula* and *Pliocathaica gansuica* together with *Pseudiberus zenonis* and *Euhadra stictotaenia* (PP = 1.00 BI, 91% ML, 91% MP). These two groups form sister groups in the tree, with *Bradybaena brevispira* falling immediately outside of this grouping.

Each species attributed to *Cathaica s.s.* forms its own branch in all trees produced with different analytical methods. The widespread species *C. pyrrhozona* has very strong support in all three methods of phylogeny construction (PP = 1.00 BI, 99% ML, 99% MP). The other widespread species, *C. Fasciola*, is also reasonably well supported (PP = 0.88 BI, 77% ML, 59% MP) though bootstrap support in the MP tree is low. Each species of *Cathaica s.s.* from Mount Tai and adjacent mountain regions is highly supported; *C. sp2* has very high support (BI = 1.00, ML = 100%, MP = 99%), *C. fohuiensis* good support (BI = 0.99, ML = 78%, MP = 77%) and *C. leei* has good support in both BI and in ML and MP trees (BI = 0.96, ML = 86%, MP = 71%). *Cathaica multicosata* sp. nov. from the Yimeng Mountains Chain is highly supported (PP = 1.00 BI, 100% ML, 96% MP) and forms the sister group of all other *Cathaica s.s.* species. (PP = 1.00 BI, 64% ML, 99% MP). *Pliocathaica buwigneri* is monophyletic with full support (PP = 1.00 BI, 100% ML, 100% MP) and forms the sister clade of *Cathaica s.s.* However, *Pliocathaica* as currently delimited is not monophyletic as other *Pliocathaica* species cluster either with *Pseudiberus* or with *Euhadra*. *Pliocathaica pulveratricula* (PP = 1.00 BI, 100% ML, 100% MP) and *Pseudiberus* are sister taxa in the tree, with this grouping highly supported in BI and ML trees (BI = 1.00, ML = 90%, MP = 47%). *Euhadra* is the sister group of *Pliocathaica pulveratricula* and *Pseudiberus* in all tree topologies, though support is not high (BI = 0.76, ML = 53%, MP = 21%). *Pliocathaica gansuica* is the sister lineage of all remaining members of the *Pseudiberus/Euhadra* clade with high statistical support (BI = 1.00, ML = 91%, MP = 91%).

TAXONOMIC-LEVEL DELIMITATION

Based on the ASAP analysis with the lowest score for the concatenated 16S and ITS2 genes (ASAP score 1.5, $P = 1.059190e-02$), the *Cathaica s.s.* species complex is delimited into eight groups corresponding to *C. fasciola*, *C. pyrrhozona*, *C. leei*, *C. multicosata*, *C. sp1*, *C. sp2* and *C. fohuiensis*, which is in turn split into two groups. However, there is no additional evidence from character homology to support the split of *C. fohuiensis* sp. nov. into two groups. The *Pliocathaica* species are delimited into three groups corresponding to *Pliocathaica buwigneri*, *Pliocathaica gansuica* and

Pliocathaica pulveratricula. We note that the second lowest ASAP result (ASAP score 2.0, $P = 4.071856e-01$) matches our results perfectly with *Cathaica s.s.* split into seven groups comprising *C. fasciola*, *C. pyrrhozona*, *C. leei*, *C. multicosata*, *C. fohuiensis*, *C. sp1* and *C. sp2* and with the *Pliocathaica* species split into three groups comprising *Pliocathaica buwigneri*, *Pliocathaica gansuica* and *Pliocathaica pulveratricula*. The genetic distances used by ASAP are shown in [Supporting Information Table S3](#).

mPTP results based on 16S using both the MCMC and ML methods suggest the same solution as the lowest ASAP-score result (both ML and MCMC LRT $P < 0.01$). As noted above, there is no additional evidence from morphology supporting the division of *C. fohuiensis* sp. nov. into two groups. For the mPTP results based on ITS2, both MCMC and ML methods suggest *Cathaica s.s.*, *Pliocathaica buwigneri*, *Pliocathaica gansuica* and *Pliocathaica pulveratricula* as separate groups (both ML and MCMC LRT $P < 0.01$). These results separate *Pliocathaica buwigneri* from *Cathaica s.s.*, though *Pliocathaica buwigneri* clusters with *Cathaica s.s.* as the sister group in the phylogenetic tree.

CHARACTER MAPPING

The morphological characters are shown mapped onto the phylogenetic tree in [Figure 7](#). Apomorphic characters are distributed as follows. The absence of poly-layered structures (PLs) in the proximal accessory sac ([Wu, 2004](#): fig. 12; [Zhang et al., 2021](#)) is an apomorphic character of the branch to *Pliocathaica gansuica*, *Pliocathaica pulveratricula* and *Pseudiberus* spp. The presence of an epiphallic papilla and an accessory sac ([Wu, 2004](#): fig. 12) are apomorphic characters of *Pliocathaica gansuica*, while cross interlocked penial pilasters ([Zhang et al., 2021](#); [Supporting Information, Fig. S17C](#)) are apomorphic characters of *Pseudiberus* spp. and *Pliocathaica pulveratricula*. Likewise, entrance(s) of the proximal accessory sac leading to the atrium ([Fig. 4F](#)) is an apomorphic character of *Pliocathaica pulveratricula*. The proximal accessory sac on the right side of the dart sac ([Fig. 4A–D](#)) is an apomorphic character of *Cathaica*. The basal expanded vagina ([Fig. 4C](#)) is the apomorphic character for *C. fohuiensis*.

Homoplastic characters are distributed at both genus and species levels. The entrance(s) of mucous glands leading to the dart sac chamber ([Fig. 4F](#); [Zhang et al., 2021](#)) is a homoplastic character for *Pseudiberus* spp. and *Pliocathaica pulveratricula*. The presence of a single proximal accessory sac and mucous glands proximally and tightly attached to the vagina ([Fig. 4F](#)) are homoplastic characters for *Pliocathaica pulveratricula*. A single proximal accessory sac ([Fig. 4B–E](#)) is a homoplastic character

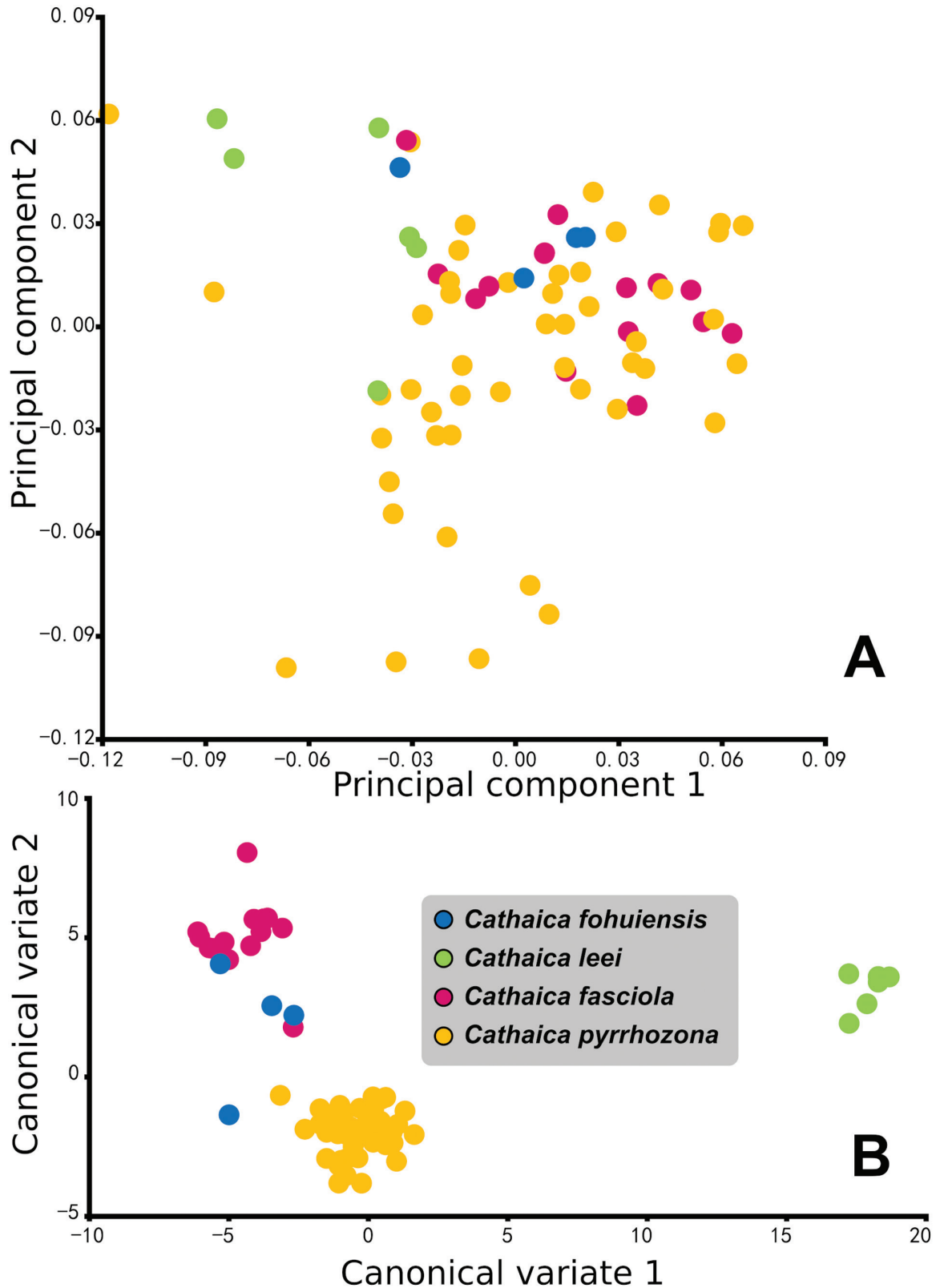


Figure 5. Scatter plots of principal component analysis (A) and canonical variate analysis (B) scores based on the data from apertural views of the *Cathaica* s.s. species from Shandong. PC1 explains 36.925% and PC2 explains 31.319% of the total shape variation of shells. CV1 explains 72.192% and CV2 explains 20.400% of the total shape variation of shells.

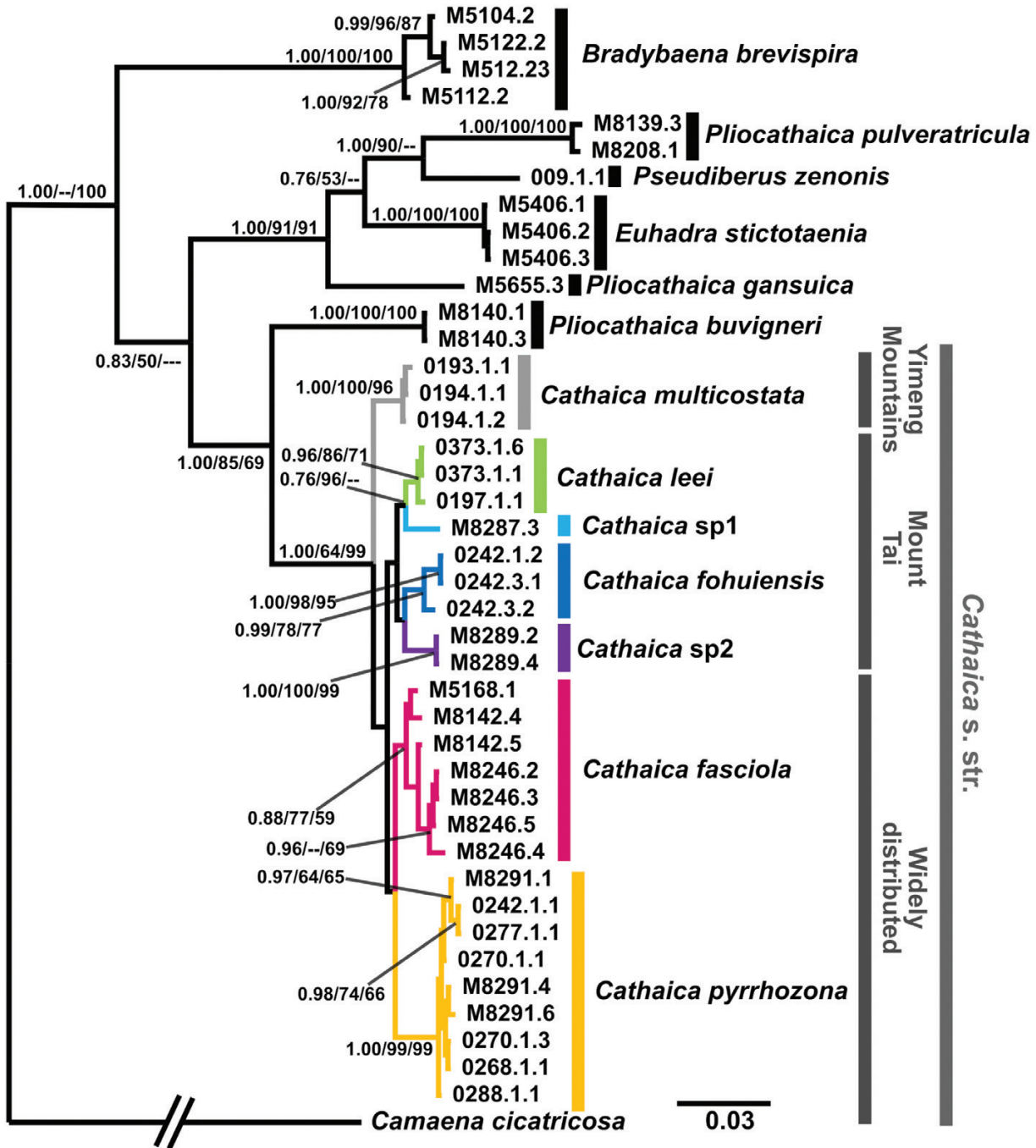


Figure 6. Bayesian inference phylogenetic tree of *Cathaica* species from Shandong together with *Pliocathaica*, *Pseudiberus*, *Euhadra* and *Bradybaena* based on a concatenated dataset of partial 16S and ITS2 sequences. The tree is rooted on the outgroup *Camaena cicatricosa*. Bayesian posterior probabilities and bootstrap values are given in the following order: BI/ML/MP. BI posterior probabilities lower than 0.70 and ML/MP bootstrap values lower than 50% are not shown. For the MP tree, CI = 0.701 and RI = 0.871. Numbers within groups are specimen numbers.

for *Pliocathaica buvigneri* and *Cathaica*. Likewise, the entrance(s) of mucous glands leading to the dart sac chamber (Fig. 4A–D) is a homoplastic character

for *Cathaica* and the double proximal accessory sac (Fig. 4A) is a homoplastic character for *Cathaica fasciola*.

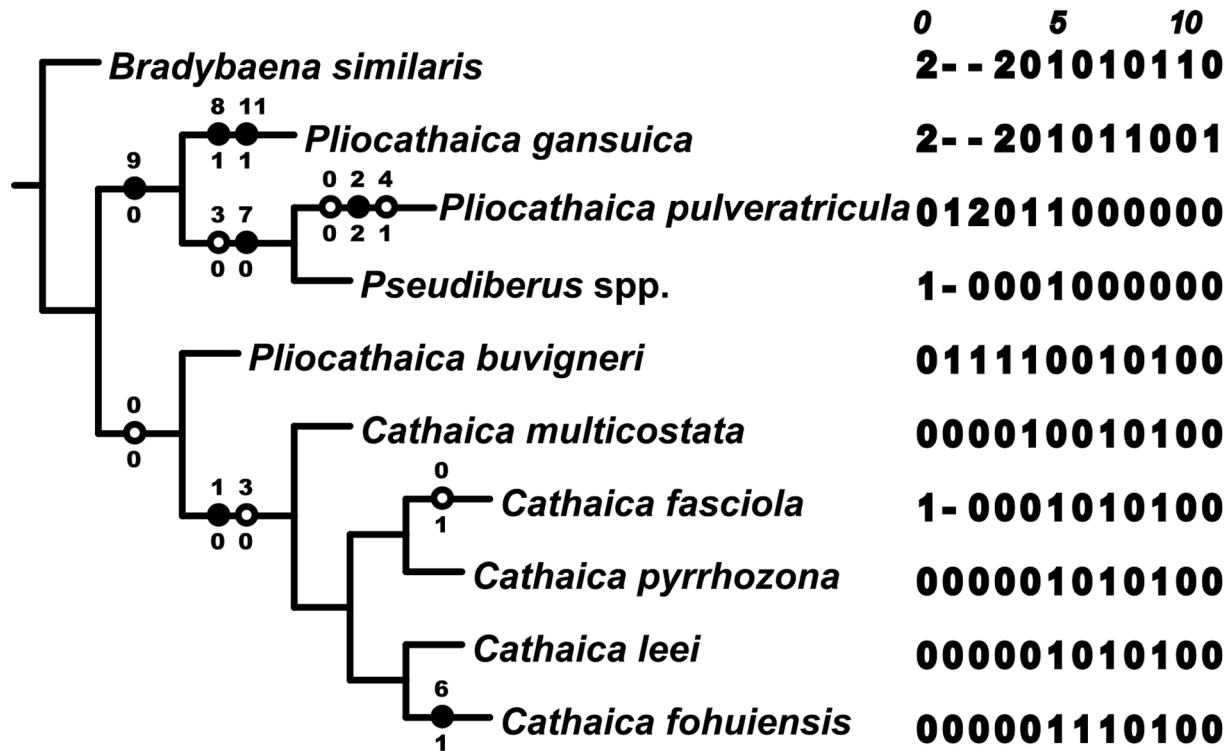


Figure 7. Mapping of morphological characters onto the molecular tree from Figure 6. The upper number on each branch is the morphological character. The lower number on each branch is the status of that character. The matrix of characters is listed for the corresponding taxa on the tree. Italic numbers on the top of the matrix mark the position of characters 0, 5 and 10. All character descriptions and the matrix are recorded in [Supporting Information Data S1](#). Black dots indicate unambiguous apomorphic characters and white dots indicate homoplastic characters. char0: Proximal accessory sac (0) single, (1) double, (2) absent; char1: Single proximal accessory sac on which side of dart sac (0) right, (1) left; char2: Entrance of proximal accessory sac leads to (0) dart sac chamber, (1) dart chamber, (2) atrium; char3: Entrance of mucous glands leads to (0) dart sac chamber, (1) dart chamber, (2) accessory sac chamber; char4: Mucous glands (0) not tight, (1) tight; char5: Vagina open to (0) dart chamber, (1) atrium; char6: Vagina basal (0) not expanded, (1) expanded; char7: Penial pilasters (0) cross interlocked, (1) parallel; char8: Epiphallic papilla (0) absent, (1) present; char9: Poly-layered structure (0) absent, (1) present; char10: Distal vagina membranous near atrium (0) absent, (1) present; char11: Accessory sac (0) absent, (1) present.

DISCUSSION

Cathaica was subdivided into four subgenera by [Andreae \(1900\)](#) based on thick (*Pliocathaica*) or thin (*Xerocathaica*, *Campylocathaica*, *Cathaica s.s.*) shells, absence (*Cathaica s.s.*, *Pliocathaica*) or presence (part of *Xerocathaica*, *Campylocathaica*) of a keel, narrow (*Pliocathaica*) or comparatively wide (*Cathaica s.s.*, *Xerocathaica*, *Campylocathaica*) umbilicus, reflected (*Pliocathaica*, *Campylocathaica*) or un-reflected (*Cathaica s.s.*, *Xerocathaica*) aperture, and absence (*Xerocathaica*, *Campylocathaica*) or presence (*Cathaica s.s.*, *Pliocathaica*) of a basal tooth. This treatment was subsequently followed by [Richardson \(1983\)](#) and [Chen & Zhang \(2004\)](#). The subgenus *Pliocathaica* was subsequently raised as a genus by [Wu \(2004, 2019\)](#).

However, while *Cathaica s.s.* is monophyletic in our phylogenetic tree, *Pliocathaica* is not and is thus not supported as a distinct genus. Instead, *Pliocathaica* is split into three groups; *Pliocathaica buvigneri* is the sister group of *Cathaica s.s.* and *Pliocathaica pulveratricula* and *Pliocathaica gansuica* cluster with *Pseudiberus* and *Euhadra* (Fig. 6). According to previous treatments (e.g. [Gude, 1902a](#)), *Pliocathaica buvigneri*, *Pliocathaica pulveratricula* and *Pliocathaica gansuica* were assigned to *Pliocathaica*. The molecular tree presented here, however, does not support this. Considering that apomorphic characters exist on the branch *Cathaica s.s.* instead of *Cathaica s.s.* plus *Pliocathaica buvigneri*, this suggests that *Pliocathaica buvigneri* does not belong to *Cathaica s.s.*

In *Cathaica* s.s. five species were recognized in Shandong Province. Three species, *C. pyrrhizona*, *C. fasciola* and *C. leei*, have been described previously and are re-described here based on type specimens. Two new species, *C. fohuiensis* sp. nov. and *C. multicostata* sp. nov. are described here for the first time.

Previously, *C. pyrrhizona* has been treated either as a subspecies or a synonym of *C. fasciola* (Suzuki, 1939; Chen & Zhang, 2004) since no differences in shell morphology have been identified. The systematic significance of differences in the reproductive anatomy of *C. pyrrhizona* and *C. fasciola* has not been recognized. However, *C. fasciola* has been considered to be widely distributed (Pilsbry, 1894; Möllendorff, 1899; Andreae, 1900; Chen & Zhang, 2004). However, GM results showed that *C. pyrrhizona* has more variable shells. Other than one specimen of *C. fasciola*, specimens collected from Shandong were *C. pyrrhizona*. That Shandong was recorded as a locality of *C. fasciola* (Möllendorff, 1899; Chen & Zhang, 2004) may be due largely to misidentifications owing to their genitalia not having been examined. Here we found *C. pyrrhizona* and *C. fasciola* are sister groups sharing similar conchological characteristics, although *C. pyrrhizona* has a single proximal accessory sac and *C. fasciola* has double proximal accessory sacs. Considering the situation of type specimens, we have designated the neotype for *C. pyrrhizona* to make the taxonomic position clear.

Cathaica leei can be clearly distinguished from other *Cathaica* species based on its plate spiral whorl and wide umbilicus. However, specimens of *C. leei* collected from the foot of Mount Tai (Shandong Yaoxiang National Forest Park) are rather unusual as the shells of these specimens all have higher spires and lower density ribs.

The newly described species *C. fohuiensis* has a higher spire and can be distinguished from other *Cathaica* s.s. by an expanded base of the vagina.

In the newly described species *C. multicostata*, the genital system is distinct from that of other *Cathaica* species in that the vagina connects to the sac chamber instead of the atrium. The mucous glands are attached tightly, proximally to the vagina before joining the dart sac, and the septa are much shorter than in other *Cathaica* s.s. The shell morphology is similar to that of *C. mengi*. The extremely depressed shells usually occur in areas of limestone and the reason for this shell shape may be related to this environment. As with *Nanotrachia* Köhler & Criscione, 2013, which inhabits an arid environment in Australia, some *Cathaica* members also have a depressed shell with dense ribs. The tendency of *Cathaica* shells to have a depressed shape and dense ribs is also observed in semi-arid inland provinces of China, such as in areas of Shanxi Province where *C. mengi* occurs. However,

C. multicostata is distinguished from other *Cathaica* s.s. in having a wide umbilicus, almost horizontal apex and sparse ribs on the thin shell, and hence it is named as a new species.

Cathaica sp1 and *C. sp2* are not formally described and named as new species owing to the lack of adequate specimens. Only one sexually immature individual was identified as *C. sp1*, which prevented a comparison of genital features. Only two individuals of *C. sp2* were involved, and more specimens are needed for a comparison of genital system variation. *Cathaica* sp1 forms the sister group of *C. leei* in the phylogenetic tree. *Cathaica* sp2 is the sister group of *C. fohuiensis*.

Cathaica pyrrhizona is widely distributed in Shandong, especially in cities and other anthropogenic environments; *C. leei* occurs at higher altitudes of Mount Tai (usually above 800 m a.s.l.). *Cathaica fohuiensis* occurs above 340 m a.s.l. on Fohui Mountain (adjacent to Mount Tai). Specimens of *C. multicostata* were collected from rocks above 340 m a.s.l. on the Baodugu (Yimeng Mountains) (Fig. 8).

The genital anatomy of species that have been attributed to *Pliocathaica* differs from that of *Cathaica* s.s. *Pliocathaica buvigneri* and *Pliocathaica pulveratricula* differ from *Cathaica* s.s. in the direction of the proximal accessory sac and in where the sac enters the vagina. *Pliocathaica gansuica* can be distinguished from *Cathaica* s.s. as it has an accessory sac instead of a proximal accessory sac, shorter penial sheath and epiphallid papilla (Wu, 2004).

The entrance of the proximal accessory sac of *Pliocathaica buvigneri* leads to the dart chamber, and in *Pliocathaica pulveratricula* the entrance to the proximal accessory sac leads to the dart sac chamber. In addition, the vagina of *Pliocathaica buvigneri* leads to the opening of the dart chamber, as in *C. multicostata*. *Pliocathaica pulveratricula*'s entrance leads to the atrium.

In *Pliocathaica pulveratricula* the penial pilasters are similar to those of *Pseudiberus* and not parallel as with other *Cathaica* s.s. members and the penial tissue is more delicate than that of *Pliocathaica buvigneri* (e.g. Wu, 2004). *Pliocathaica pulveratricula* is the sister group of *Pseudiberus*. Hence, the penial tissue may be the symplesiomorphy of this species group. Unfortunately, the type species of *Pliocathaica*, *Pliocathaica pulveratrix*, is not included in our phylogenetic study. Therefore, we are unable to remove the prevailing uncertainty on the phylogenetic position of *Pliocathaica*.

The phylogeny and taxonomic delimitation data based on ITS2 resolve *Cathaica* s.s. as one group and the three *Pliocathaica* species, *Pliocathaica pulveratricula*, *Pliocathaica gansuica* and *Pliocathaica buvigneri*, as three separate groups. This suggests that the three *Pliocathaica* species should be divided

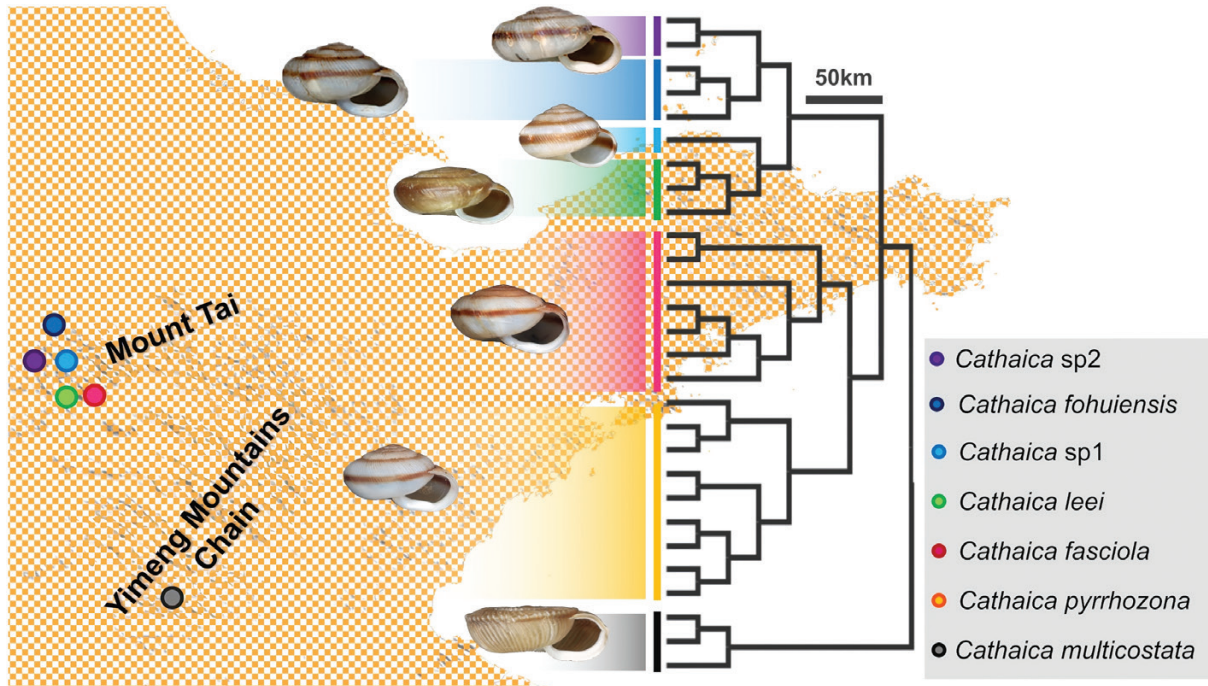


Figure 8. Geographical and phylogenetic relationships of *Cathaica* species in Shandong. Phylogenetic tree taken from Figure 6. *Cathaica fasciola* (Draparnaud, 1801) is considered a widely distributed species, but the morphological and molecular evidence indicates that it has a limited distribution in Shandong based on current specimens. The distribution of the widely distributed species *C. pyrrhozona* (Philippi, 1847) is marked using the orange grid.

into three genera based on the cladistic species concept. However, type species need to be examined to confirm which *Pliocathaica* group should be the real *Pliocathaica* (*Pliocathaica* *is.s.*). Here, we use three informal names to represent these three genera-level taxa, aff. *Pliocathaica* for *Pliocathaica pulveratricula*, Richthofeni-A (Richthofeni group from Andreae, 1900) for *Pliocathaica buvigneri* and Richthofeni-B for *Pliocathaica gansuica*.

Previously, the presence or absence of genital characters were considered as an unstable character for diagnosing Bradybaeninae genera (Hirano *et al.*, 2014). Hirano *et al.* (2014) considered that even species within Bradybaeninae genera obtained and lost their genital organs several times during the evolutionary process. Based on current studied genus-level taxa (*Bradybaena*, *Euhadra*, *Pseudiberus*, *Cathaica*, aff. *Pliocathaica*, Richthofeni-A and Richthofeni-B), gain and loss of genital characteristics are only found between genera and not between species. This hypothesis matches the hypothesis of genital system evolution at the genus level shown by the results from Beese *et al.* (2009) and Wu (2004, 2019). Based on studied genus-level taxa, unambiguous apomorphic characters are a sufficient and necessary condition for the establishment of a single genus. This

finding would also benefit taxonomic-level checks. The proximal accessory sac is a special organ; *C. fasciola* gains another proximal accessory sac, while its sister group has one proximal accessory sac. The direction of the proximal accessory sac is also important at the genus level.

Based on the studied taxa, the relative connection of genital organs (e.g. where the opening of the proximal accessory sac leads to) are rapidly evolving among species in a single genus. The evolution of genital characteristics among species in one genus is probably caused by environmental pressure. For example, *C. fasciola* has double proximal accessory sacs.

SYSTEMATIC ACCOUNT OF *CATHAICA* S.S.

HELICOIDEA RAFINESQUE, 1815

CAMAENIDAE PILSBRY, 1895

BRADYBAENINAE PILSBRY, 1898

CATHAICA MÖLLENDORFF, 1884

Type species: *Helix pyrrhozona* Philippi, 1847, by original designation.

Helix (Cathaica) Möllendorff, 1884: 339.

Helix (Cathaica) Pilsbry, 1892: 204; Pilsbry 1894: 200, 202, 205.

Cathaica (Eucathaica) Andreae, 1900: 3; Gude, 1902a: 8, 1902b: 52.

Cathaica, Thiele, 1931: 692; Yen, 1939: 137 (*Helix fasciola* Draparnaud cited as type species in error); Zilch, 1960: 636; Schileyko, 2004: 1690.

Diagnosis: Embryonic shell granulated. Penial sheath, proximal accessory sac(s) present. Mucous glands more than two. Epiphallic papilla, penial caecum, flagellum, membranous sac surrounding terminal genitalia or accessory sac, poly-layered structure absent.

Remarks: Internal structures of the dart apparatus have been widely neglected in the subfamily Bradybaeninae. For example, *C. fasciola* lacks the poly-layered structure (PL) that is characteristic in the dart sac trunk in some other Bradybaeninae taxa such as *Bradybaena* and *Aegista* (Wu, 2004, 2019). Correctly distinguishing the accessory sac from the proximal accessory sac is critical. The accessory sac is an expanded tube of varying volume connecting the mucous glands with the dart sac whereas the proximal accessory sac is a caecum membrane located on and only opening into the dart sac.

The genital characters of species in the subgenus *Cathaica* that occur in Shandong Province are as follows. Membranate sac surrounding terminal genitalia absent. Penial sheath long. Penis long; slender; externally simple. Penial pilasters undifferentiated. Epiphallic papilla absent. Flagellum lacking. Mucous glands proximally attached to vagina tightly before entering dart sac; opening into dart sac chamber. Proximal part of dart sac not forming neck-structure (Wu, 2004). Dart sac containing one dart. Proximal accessory sac on right side of dart sac; internally with numerous parallel septa.

Type material of the type species has not been located (Coan & Kabat, 2017) and the neotype is designated in material examined of section *Cathaica pyrrhozona*.

CATHAICA FASCIOLA (DRAPARNAUD, 1801)

(FIGS 1, 3A–B, 4A, 5, 6)

Helix fasciola Draparnaud, 1801: 87; Tryon 1887: 208, pl. 47, figs 57–59.

Eulota (Cathaica) fasciola, Pilsbry 1894: 206.

Cathaica fasciola, Möllendorff 1899: 58.

Cathaica (Eucathaica) fasciola, Andreae 1900: 3, pl. 1, figs 1, 2.

Cathaica fasciola fasciola, Yen 1939: 138, pl. 14, fig. 20.

Cathaica (Cathaica) fasciola fasciola, Zilch 1968: 158; Chen & Zhang 2004: 218–220, fig. 193.

Cathaica (Cathaica) fasciola, Wu 2004: 92, 102, fig. 22; Schileyko 2004: 1690–1691, fig. 2182.

Diagnosis: Shell depressed. Spire with fine ribs. Umbilicus tiny. Mucous glands numerous; complicatedly branched; entering love dart chamber. Proximal accessory sacs two, sub-equally developed bilaterally. Openings of proximal accessory sacs and mucous glands enter into chamber containing love dart. Vagina entering atrium rather than entering dart sac chamber.

Material examined: Previous holotype: NHMW-MO-14383 (Vinarski & Eschner, 2016). Museum material: NHMUK 1912.6.27.45; SMF22861a; NHMUK 1921.10.6.48–50. Other material: Woyang, Bozhou, Anhui Province, 15 FMA, 33.545°N, 116.213°E, 29 m a.s.l., July 2017, coll. X. Sheng, HBUMM8142-spec.1–15; Qingyang, Gansu Province, nine FMA, 35.738°N, 107.701°E, 1353 m a.s.l., July 2017, coll. X. Sheng; Fohui Mountain, Jinan, SDP, one FMA, 36.639°N, 116.999°E, 158 m a.s.l., 20 May 2018, coll. Zhang G., Qi J., Zhang J., Zhao X., SDNU.Gas.0277.01.10; HBUMM8144-spec.2–9; Yingxiong Mountain, Jinan, SDP, one FMA, 36.638°N, 116.999°E, 167 m a.s.l., 26 May 2018, coll. Zhang G., Qi J., Zhao X., SDNU.Gas.0278.02.01; HBUMM8144-spec.1; Yingxiong Mountain, Jinan, SDP, one FMA, 36.638°N, 116.999°E, 167 m a.s.l., 26 May 2018, coll. Zhang G., Qi J., Zhao X., SDNU.Gas.0278.02.01. All specimens included in other material were dissected.

Re-description: Shell. Depressed, thin, dextral. Whorls convex. Umbilicus narrow to slit-like. The transition to the base of the umbilicus is abrupt. Columella oblique. Columellar lip dilated, slightly covering or covering half umbilicus. Protoconch with radially arranged elongate granules. Spiral furrows generally absent. Body whorl straight or slightly descending in front. Aperture oblique; somewhat sinuate at peristome. Shell surface smooth. Growth lines clear, not accompanied by irregular thickenings. Young shell rough, angulated. Adult shell smooth. Teleoconch without microscopic structure. Adult body whorl rounded at periphery or slightly bluntly angulate supra-peripherally. Ventral side convex. Aperture rectangular, internally with ring-like thickening. One distinct or sometimes indistinct broad but very low parietal basal tooth near columella. Peristome thin, not continuous. Callus indistinct. Shell white or off white; with one peripheral reddish-brown band; a broader brownish band adjacent to suture on body whorl sometimes present. Shell width 14.8 ± 1.0 mm. Shell height 9.1 ± 0.6 mm.

General anatomy. Dorsum and sole creamy white; eversible head wart brownish to yellow; ommatophores

low but distinct when retracted. Mantle edge without lobed appendage. Jaw arcuate; with approximately nine more or less projecting ribs.

Genitalia. Membranate sac surrounding terminal genitalia absent. Penial sheath long. Penis long, very slender, simple externally. Penial pilasters undifferentiated. Epiphallic papilla and flagellum absent. Vas deferens thickened near penial retractor. Six mucous glands, shorter than dart sac, each with distinct peduncle, complicatedly branched, enter love dart chamber. Vaginal region between dart sac and atrium short. Proximal part of dart sac not forming neck-structure. Dart sac with one dart. Love dart curved; basally unexpanded; cross-section circular. Two proximal accessory sacs connected proximally on dart sac; sub-equally developed; the right sac may be significantly larger (only seen in one specimen SDNU.Gas.0278.02.01); each with one opening to chamber containing love dart; internally with numerous parallel septa. Openings of proximal accessory sacs entering chamber containing love dart. Vagina entering atrium rather than entering dart sac chamber, proximally unexpanded. Measurements: PS + P 9.7 mm; VD 15 mm; PR 3 mm; Va 11.9 mm; BC + BCD 9.3 mm; DS 6.5–6.8 mm; PAS 1.7–4.2 mm; MG 4.9–8.1 mm.

Distribution: Beijing, Tianjin, Hebei, Shandong, Shanxi, Shaanxi, Gansu, Sichuan, Hubei, Hunan, Jiangsu, Shanghai [type locality: Chine (China)].

Ecology: This species and related species are common and locally abundant in northern China and frequently inhabit human-transformed habitats.

Remarks: Of the *Cathaica* species examined to date, *C. fasciola* is the only species possessing two proximal accessory sacs rather than a single sac. Other examined species possess one opening leading to the dart sac chamber/love dart chamber that is unconnected to the mucous glands. In contrast to the proximal accessory sac, the accessory sac is a structure connecting and always situated between the mucous glands and dart sac chamber/love dart chamber. Therefore, in *C. fasciola* and the other *Cathaica* spp. mentioned in this paper there is no true accessory sac. In the phylogenetic analysis, this species is the sister group of *C. pyrrhozona* but without high bootstrap support.

An examination of type material revealed an indistinct keel present on the upper half of the body whorl. A slight keel is present in type specimens.

CATHAICA PYRRHOZONA (PHILIPPI, 1847)

(FIGS 1, 3C, 4B, 5, 6)

Helix pyrrhozona Philippi, 1847: 28, pl. 6, fig. 4; Pfeiffer 1860: 73, pl. 79, figs 7–9; Debeaux 1868: 244;

Möllendorff 1881: 38; Heude 1882: 43, pl. 16, figs 7, 8; Gredler 1878: 104; Gredler 1882: 47; Ping 1929: 7, 15, figs 1a, 1b.

Helix (Cathaica) pyrrhozona, Möllendorff 1884: 339, 341; Pilsbry 1892: 204, pl. 47, figs 60–63.

Eulota (Cathaica) pyrrhozona, Pilsbry 1894: 205, pl. 65, figs 7, 8, pl. 66, fig. 32; Ping 1931: 20, figs 9a–9c.

Cathaica pyrrhozona, Blume 1925: 11; Wiegmann 1900: 142.

Diagnosis: Shell depressed. Spire with fine ribs. Umbilicus small. Mucous glands numerous; simply branched. Proximal accessory sac one; on right side of dart sac. Openings of proximal accessory sac and mucous glands leading to dart sac chamber. Vagina entering atrium.

Material examined: Neotype: one FMA, 36.627°N, 117.046°E, 366 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, registered voucher no. SDNU.Gas.0292.01.01. Other materials: Yangtian Mountain, Weifang, SDP, five FMA, 36.461°N, 118.278°E, 643 m a.s.l., 6 April 2018, coll. GZ, SDNU.Gas.0130.02.01–05; Yunmen Mountain, Weifang (Qingzhou), SDP, ten FMA, 36.643°N, 118.455°E, 296 m a.s.l., 7 April 2018, coll. GZ, SDNU.Gas.0156.03.01–10; Yunmen Mountain, Weifang (Qingzhou), SDP, six FMA, 36.643°N, 118.455°E, 301 m a.s.l., 7 April 2018, coll. GZ, SDNU.Gas.0157.03.01–06; Yuan Mountain, Zibo, SDP, five FMA, 36.481°N, 117.841°E, 385 m a.s.l., 12 May 2018, coll. GZ, SDNU.Gas.0205.02.01–05; Dezhou, SDP, 11 FMA, 37.43°N, 116.33°E, coll. Y. Zou, HBUMM8290-spec.1–11; Fohui Mountain, Jinan, SDP, one FMA, 36.638°N, 116.993°E, 50 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0262.01.08; Fohui Mountain, Jinan, SDP, one FMA, 36.638°N, 116.993°E, 67 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0263.01.03; Fohui Mountain, Jinan, SDP, one FMA, 36.638°N, 116.993°E, 69 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0266.01.01; Fohui Mountain, Jinan, SDP, one FMA, 36.639°N, 116.994°E, 62 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0269.01.08; Fohui Mountain, Jinan, SDP, three FMA, 36.639°N, 116.995°E, 69 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0270.01.01–03; Fohui Mountain, Jinan, SDP, two FMA, 36.638°N, 116.995°E, 78 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0272.01.01–02; Fohui Mountain, Jinan, SDP, three FMA, 36.639°N, 116.995°E, 58 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0273.01.01–03; Fohui Mountain, Jinan, SDP, nine FMA, 36.639°N, 116.999°E, 158 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0277.01.01–09; Fohui Mountain, Jinan, SDP, one FMA, 36.635°N, 116.999°E, 107 m a.s.l., 20 May 2018,

coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0283.02.01; Fohui Mountain, Jinan, SDP, one FMA, 36.634°N, 116.998°E, 126 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0287.01.01; Fohui Mountain, Jinan, SDP, two FMA, 36.634°N, 116.998°E, 110 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU.Gas.0288.01.01–02; Fohui Mountain, Jinan, SDP, one FMA, 36.638°N, 116.994°E, 88 m a.s.l., 26 May 2018, coll. GZ, J. Qi, X. Zhao, SDNU.Gas.0268.01.01; Meny Mountain, Jinan, SDP, four FMA, 36.534°N, 117.096°E, 414 m a.s.l., 11 May 2019, coll. GZ, J. Qi, registered voucher nos. HBU MM 8314-spec.1–4; Fohui Mountain, Jinan, SDP. All specimens are dissected.

Re-description: Shell depressed, thin, dextral. Suture impressed. Umbilicus narrow, partially covered by columellar lip. Bottom–umbilicus transition changed gently. Columella oblique. Columellar lip dilated. Protoconch finely granulated. Spiral furrows absent. Aperture oblique; somewhat sinuate at peristome. Spire whorls with ribs. Peripheral crenulation formed by ribs indistinct. Growth lines indistinct; not accompanied by irregular thickenings. Young shell rough; angulated. Adult shell smooth. Teleoconch without other microscopic structure. Adult body whorl rounded at periphery; with convex base. Aperture rectangular. Aperture internally thickened; with one low and broad basal tooth. Peristome thin. Callus indistinct. Shell brownish white; with one thick chestnut peripheral band. Shell width 14.1 ± 0.6 mm. Shell height 8.7 ± 0.6 mm.

General anatomy. Retracted head wart between ommatophore indistinct. Mantle edge without any lobed appendage. Jaw arcuate; with 6–8 more or less projecting ribs.

Genitalia. Membranate sac surrounding terminal genitalia absent. Penial sheath long. Penis long; slender; simple outside. Penial pilasters undifferentiated. Epiphallallic papilla absent. Flagellum lacking. Vas deferens thickened near penial retractor. Mucous glands approximately 6 (5–7); subequal to dart sac in length; each with distinct peduncle, simply branched. Vaginal region between dart sac and atrium short. Proximal part of dart sac not forming neck-structure. Dart sac containing one love dart. Love dart curved; basally unexpanded. Proximal accessory sac on right side of dart sac; internally with numerous parallel septa. Openings of proximal accessory sac and mucous glands entering chamber containing love dart. Vagina entering atrium rather than entering dart sac chamber, proximally unexpanded. Measurements: PS + P 10.5 mm; VD 20 mm; PR 7.6 mm; Va 25.7 mm;

BC + BCD 15.4 mm; FO unknown; DS 5.6 mm; PAS 1.9 mm; MG 5.1 mm.

Ecology: In Jinan, this species has a high population density and is frequently found in anthropogenic habitats.

Distribution: Shandong (Jinan City, Tai'an City); Shanghai City (type locality: Ji nan, Shandong).

Remarks: Original type specimens of *Helix pyrrhizona* could not be located [Coan & Kabat, 2017; Ronald Janssen (SMF) pers. comm.; Christine Zorn (Museum für Naturkunde, Berlin) pers. comm.; Jon Ablett (NHMUK) pers. comm.; Virginie Héros (NHM, Paris) pers. comm.; Meng Kaibaryer (Chinese Academy of Sciences, Beijing) pers. comm.] and are deemed to be lost. A neotype is designated herein in accordance with Article 75 of the International Code of Zoological Nomenclature (ICZN, 1999) to clarify the taxonomic status and the type locality of this taxon and to aid its identification. *Cathaica pyrrhizona* cannot be distinguished from *C. fasciola* based on conchological characters alone and knowledge of the soft body is necessary to distinguish both species (for differences between both species see further below).

Based on divergent features ranging from shell morphology, the genital system and molecular evidence (Figs 3A–C, 4–6), we present robust evidence that *C. fasciola* and *C. pyrrhizona* are distinct species. In the basic illustration of the genitalia of '*Eulota pyrrhizona*' provided by Pilsbry (1894: pl. 66, fig. 32), the absence of the right proximal accessory sac is evidence that Pilsbry was dealing with a different species. This was possibly *C. fohuiensis* Zhang sp. nov., which shares the expanded proximal vagina shown in Pilsbry's figure.

The shells of *C. pyrrhizona* vary greatly among different geographical populations and are difficult to distinguish from those of *C. fasciola*. Generally, the periphery of *C. pyrrhizona* is much rounder than that of *C. fasciola*; however, this is not a consistent difference and we have not identified a reliable feature that allows shells of these two species to be distinguished.

CATHAICA LEEI YEN, 1935

(FIGS 1, 3D, 4B, 5, 6)

Cathaica leei Yen, 1935: 39–40, pl. 3 figs 4–4b.

Diagnosis: Shell depressed. Spire without ribs. Umbilicus broad. Mucous glands numerous; simply branched; opening to dart sac chamber. Single proximal accessory sac; on right side of dart sac. Openings of

proximal accessory sac leading to dart sac chamber. Vagina opening to atrium.

Material examined: Holotype: Taian, SDP, coll. E. Licent, THZ015034. Paratypes: Taian, SDP, coll. E. Licent, THZ015035; Taian, SDP, coll. E. Licent, registered voucher no. THZ015036; coll. E. Licent, THZ015037. Other materials: Mount Tai, Taian, SDP, six FMA, 36.256°N, 117.104°E, 1471 m a.s.l., 6 October 2018, coll. GZ, SDNU.Gas.0373.01.01–06, two specimens are dissected; Mount Tai, Taian, SDP, one FMA, 36.245°N, 117.109°E, 753 m a.s.l., 6 October 2018, coll. GZ, SDNU.Gas.0371.01.01; Mount Tai, Taian, SDP, three FMA, 36.256°N, 117.103°E, 1480 m a.s.l., 6 October 2018, coll. GZ, SDNU.Gas.0289.01.01–03.

Re-description: Shell depressed, thin, dextral. Whorls convex. Suture superficial. Umbilicus broad. Transition of the umbilicus not abrupt. Columella vertical. Columellar lip dilated, seldom covering umbilicus. Protoconch with radical wrinkles. Spiral furrows present on spire. Aperture oblique; not sinuate at peristome. Shell surface ribless. Growth lines distinct, not accompanied by irregular thickenings. Shell imperforate. Adult shell smooth. Teleoconch without other microscopic sculpture. Young shell angulated. Adult body whorl angulate above periphery, convex below periphery. Aperture rectangular. Ring-like thickening within aperture absent. Aperture toothless, equally expanded. Peristome thin, not continuous. Shell yellowish brown, with two reddish brown bands: one above suture and one at periphery. Shell width 16.3 ± 0.8 mm. Shell height 8.1 ± 0.4 mm.

General anatomy. Retracted head wart between ommatophore distinct. Mantle edge without lobed appendage. Tentacles and dorsum leaden-black. Sole creamy white. Jaw arcuate; with 7–8 ribs.

Genitalia. Membranate sac surrounding terminal genitalia absent. Penial sheath approximately half length of penis. Penis slender; simple outside. Penial pilasters five. Epiphallic papilla and flagellum absent. Vas deferens slightly thickened near penial retractor. Mucous glands 7–8; longer than dart sac; each with distinct peduncle; simply branched; opening into dart sac chamber. Vaginal region between dart sac and atrium short. Dart sac containing 1 dart; curved; basally unexpanded. Proximal accessory sac on right side of dart sac; internally with numerous parallel septa; opening into dart sac chamber. Vagina entering into atrium, proximally unexpanded. Measurements: PS + P 10.9 mm; VD 19.6 mm; PR 2.7 mm; Va 23.8 mm; BC + BCD 20.6 mm; DS 6.2 mm; MG 10.8 mm; FO unknown; AS unknown.

Distribution: Shandong (type locality: Taishan = Mount Tai, Tai'an xian, Shandong).

Ecology: Lives on the slopes and on top of Mount Tai, usually above 800 m a.s.l. They were observed active on leaves in summer. Hibernation in rock crevices was observed in autumn.

Remarks: The species has the broadest umbilicus among Shandong *Cathaica* species.

Typical forms of this species occur at higher altitudes on Mount Tai. Some examples collected from low altitudes on Mount Tai, here attributed with the tag *C. leei* (Low alt.), are high spired with fine densely packed ribs, a narrower umbilicus and distinct basal tooth (Fig. 3D). Examples of *C. leei* (Low alt.) are mixed with *C. leei* in the molecular analysis (Fig. 5).

CATHAICA MULTICOSTATA ZHANG SP. NOV.

(FIGS 1, 3E, 4D, 5, 6)

Zoobank registration: [urn:lsid:zoobank.org:act:3609A110-2C64-44BE-8C9F-DF7281C09362](https://zoobank.org/urn:lsid:zoobank.org:act:3609A110-2C64-44BE-8C9F-DF7281C09362)

Diagnosis: Shell extremely depressed. Spire with strong ribs. Umbilicus broad. Mucous glands numerous; complicatedly branched. One proximal accessory sac on right side of dart sac. Proximal accessory sac, mucous glands and vagina opening to dart sac chamber.

Material examined: Holotype: SDNU.Gas.0193.01.01; Baodu, Zaozhuang, Shandong; 34.984°N, 117.721°E, 520 m a.s.l.; 30 April 2018; Coll. GZ, Y. Zhang, D. Li. Paratypes: two FMA, SDNU.Gas.0194.01.01–SDNU.Gas.0194.01.02; Baodu, Zaozhuang, Shandong; 34.983°N, 117.714°E, 340 m a.s.l.; 30 April 2018; Coll. GZ, Y. Zhang, D. Li. All type specimens are dissected.

Description: Shell discoid, thin, dextral. Spire very low to slightly concave. Whorls flattish. Suture superficial. Umbilicus broad. Transition to umbilicus gradual. Columella oblique. Columellar lip slightly dilated, never covering umbilicus. Protoconch highly granulate. Spiral furrows sparsely and irregular distributed on spire. Body whorl straight or slightly ascending behind aperture. Aperture oblique; sometimes somewhat sinuate at peristome. Shell surface with fine ribs, not forming crenulations at periphery. Growth lines between ribs indistinct. Young shell rough. Adult shell rough with periostracum derivatives. Teleoconch without microscopic structure. Young shell carinate. Adult body whorl supra-peripherally sharply carinate, basally convex. Aperture peach-shaped quadrate. Ring-like thickening within aperture present. Aperture toothless,

slightly or not expanded. Peristome thin, not continuous. Callus indistinct. Shell dull, in even brownish yellow, whitish behind aperture, pigmented bands absent. Shell width 16.8 ± 0.2 mm. Shell height 6.4 ± 0.5 mm.

General anatomy. Eversible head wart between ommatophore insertions low but distinct. Mantle edge without lobed appendage. Tentacles and dorsum leaden-black. Sole creamy white. Jaw arcuate; with 7–8 ribs.

Genitalia. Membranate sac surrounding terminal genitalia absent. Penial sheath long, approximately 1/3 of penis length. Penis long; slender; simple externally. Penial pilasters undifferentiated. Epiphallic papilla absent. Flagellum lacking. Vas deferens slightly thickened near penial retractor muscle. Mucous glands eight; approximately equal to dart sac in length; each with distinct peduncle; complicatedly branched; proximally attached to vagina tightly before entering dart sac; opening into dart sac chamber. Vaginal region between dart sac and atrium short about length of dart sac. Proximal part of dart sac not forming neck-structure. Dart sac containing one piece of dart, curved. Love dart cross-section diamond. Proximal accessory sac on right side of dart sac; internally with numerous parallel septa; opening into dart sac chamber near mucous gland entrance. Vagina entering dart sac chamber, unexpanded. Measurements: PS + P 15.0 mm; PR 4.6 mm; BC + BCD 15.4 mm; FS 8.5 mm; MG 5.4 mm.

Etymology: Named for its numerous thick ribs on shell.

Type locality: Shandong (Zaozhuang).

Distribution: Shandong.

Ecology: Found on rock faces near summit.

Remarks: According to descriptions of subgenera (Andreae, 1900) *C. multicosata* Zhang sp. nov. exhibits shell characters (i.e. presence of a keel) consistent with supposed characteristics of *Xerocathaica*. However, the molecular analyses revealed its closer relationships with *C. fasciola*. Shells of the species are similar to those of *Cathaica mengi* Yen, 1935 occurring in South Shanxi Province but can be distinguished with *C. mengi* having a thin flat shell, lacking a basal tooth, and having stronger and sparse ribs (Zhang *et al.*, 2020).

CATHAICA FOHUIENSIS ZHANG SP. NOV.

(FIGS 1, 3F, 4C, 5, 6)

Zoobank registration: [urn:lsid:zoobank.org:act:9C5BB804-C88E-4D0C-BECB-14A019279834](https://zoobank.org/act:9C5BB804-C88E-4D0C-BECB-14A019279834)

Diagnosis: Shell depressed. Spire with ribs. Umbilicus narrow. Mucous glands numerous; simply branched. One proximal accessory sac; on right side of dart sac. Proximal accessory sac and mucous glands opening into dart sac chamber. Vagina entering atrium; proximally expanded.

Material examined: Holotype: Fohui Mountain, Jinan, SDP, one FMA, 36.628°N, 117.048°E, 392 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU. Gas.0243.03.01. Paratypes: Fohui Mountain, Jinan, SDP, one FMA, same collection data as holotype, SDNU. Gas.0243.03.02; Fohui Mountain, Jinan, SDP, one FMA, 36.627°N, 117.048°E, 341 m a.s.l., 20 May 2018, coll. GZ, J. Qi, J. Zhang, X. Zhao, SDNU. Gas.0242.01.01. All type specimens were dissected.

Description: *Shell.* Discoid, thin, dextral. Whorls convex. Umbilicus narrow. Transition to umbilicus abrupt. Columella oblique. Columellar lip dilated, slightly covering umbilicus. Protoconch with radially arranged elongate granules. Spiral furrows absent as a rule. Body whorl slightly descending approaching the aperture. Aperture oblique; somewhat sinuate at peristome. Shell surface with ribs. Growth lines clear, not accompanied by irregular thickenings. Young shell rough, angulated. Adult shell smooth. Teleoconch without other microscopic structure. Adult body whorl rounded at periphery or slightly bluntly angulate supra-peripherally. Basally convex. Aperture rectangular, internally with ring-like thickening, with one distinct basal tooth. Peristome thin, not continuous. Callus indistinct. Shell white to dirty white; with two reddish brown bands, one peripheral and one below suture. Shell width 15.8 ± 1.3 mm. Shell height 11.1 ± 1.1 mm.

Genitalia. Membranate sac surrounding terminal genitalia absent. Penial sheath long. Penis long; slender; simple outside. Penial pilasters undifferentiated. Epiphallic papilla absent. Flagellum lacking. Vas deferens slightly thickened near penial retractor. Mucous glands approximately 4; subequal to dart sac in length; simply branched, each with a distinct peduncle. Vagina between dart sac and atrium short. Proximal dart sac not forming neck-structure. Dart sac containing one love dart. Proximal accessory sac on right side of dart sac; internally with numerous parallel septa. Openings of proximal accessory sac and mucous glands entering chamber containing love dart. Vagina entering atrium rather than entering dart sac chamber, proximally expanded. Measurements: DS = 8.2 mm; MG = 6.4 mm.

Type locality: Shandong (Jinan: Fohui Mountain).

Distribution: Shandong.

Ecology: This species lives with *C. pyrrhozona*.

Etymology: This is named after the type locality.

Remarks: This species is similar to *C. fasciola* and *C. pyrrhozona* and cannot be distinguished from these two species in GMM analysis but has a higher spiral whorl (Fig. 5); however, the base of the vagina is expanded (Fig. 3C) and this character is apomorphic for *Cathaica* s.s.

DATA AVAILABILITY

The DNA sequences generated in this study are available on the GenBank Nucleotide Database at <https://www.ncbi.nlm.nih.gov/genbank/> and can be accessed with the accession numbers OR039836–OR039875 and OR061088–OR061127 (full details of samples and accession numbers are provided in Supporting Information, Table S2).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article on the publisher's website.

Fig. S1. *Cathaica fasciola* (Draparnaud, 1801), shells: A, SDNU.Gas.277.01.10; B, SDNU.Gas.278.01.01; C–F, HBUMM8142-spec.1, 10, 15, 16.

Fig. S2. *Cathaica fasciola* (Draparnaud, 1801), shells: A, BMNH 1912.6.27.45; B, SMF22861a; C–D, BMNH 1921.10.6.48–50.

Fig. S3. Shells of *Cathaica pyrrhozona* (Philipi, 1847): A, SDNU.Gas.0292.01.01; B, HBUMM8144-spec. 1; C, HBUMM8144-spec. 2; D, HBUMM8144-spec. 3; E, HBUMM8144-spec. 4; F, HBUMM8144-spec. 5.

Fig. S4. Shells of *Cathaica leei* Yen, 1935: A, SDNU.Gas.313.01.01; B, SDNU.Gas.289.01.03; C, SDNU.Gas.289.01.01.

Fig. S5. Type specimens of *Cathaica multicostata* Zhang **sp. nov.**: A, SDNU.Gas.194.01.01, paratype; B, SDNU.Gas.193.01.01, holotype; C, SDNU.Gas.194.01.02, paratype.

Fig. S6. Genital and soft body of *Cathaica fohuiensis* Zhang **sp. nov.** A–B, general view of genitalia, both sides; C, view of mucous glands; D, anterior part of animal, dorsal view, showing the head gland between ommatophore tentacles is absent.

Fig. S7. Shells of *Pliocathaica buvigneri* (Deshayes, 1873): A, SMF23386; B–D, BMNH Ex Salisbury Acc. No. 2044; E, BMNH 91.3.7.346; F, HBUMM08140-specimen 1.

Fig. S8. Shells of *Pliocathaica subrugosa* (Deshayes, 1874): A, SMF9050, holotype of *Cathaica (Pliocathaica) subrugosa kalganensis* (Moellendorff, 1875); B, SMF9051, paratype of *Cathaica (Pliocathaica) subrugosa kalganensis*; C–D, SMF23374; E, SMF23375; F, BMNH 91.3.17.394.

Fig. S9. Shells of *Pliocathaica pulveratricula* (Martens, 1882): A–B, SMF22874; C, HBUMM08208-spec. 3.

Fig. S10. Soft body of *Cathaica fasciola* (Draparnaud, 1801): A–B, general view of genitalia, both sides; C, anterior part of animal, dorsal view, showing the head gland between ommatophore tentacles; D, view of mucous glands, the proximal accessory sac equally developed, since the distance between the two PAS are different from the lens, the dimensions look different; E–F, the leaf-shaped appendage (arrowed) on the left margin of mantle absent, in two views.

Fig. S11. Soft body of *Cathaica pyrrhozona* (Philippi, 1847): A–B, general view of genitalia, both sides; C, anterior part of animal, dorsal view, showing the head gland between tentacles absent; D, the leaf-shaped appendage (arrowed) on the left margin of mantle absent; E–G, proximal genitalia.

Fig. S12. Soft body of *Cathaica leei* Yen, 1935: A, anterior part of animal, dorsal view, showing the head gland between ommatophore tentacles; B, view of mucous glands; C–D, general view of genitalia, both sides.

Fig. S13. Type specimens of *Cathaica multicostata* Zhang **sp. nov.**: A, SDNU.Gas.194.01.01, paratype; B, SDNU.Gas.193.01.01, holotype; C, SDNU.Gas.194.01.02, paratype.

Fig. S14. Genital and soft body of *Cathaica fohuiensis* Zhang **sp. nov.** A–B, general view of genitalia, both sides.

Fig. S15. Soft body of *Pliocathaica buvigneri* (Deshayes, 1873): A, length of the dart sac is close to body length; B, anterior part of animal, dorsal view, showing the head gland between ommatophore tentacles; C–D, the leaf-shaped appendage (arrowed) on the left margin of mantle absent, in two views; E–F, general view of genitalia, both sides; G, view of mucous glands.

Fig. S16. Soft body of *Pliocathaica pulveratricula* (Martens, 1882): A, anterior part of animal, dorsal view, showing the head gland between ommatophore tentacles; B–C, the leaf-shaped appendage (arrowed) on the left margin of mantle absent, in two views.

Fig. S17. Genital system of *Pliocathaica pulveratricula* (Martens, 1882): A–B, general view of genitalia, both sides; C, interior view of penis; D, view of mucous glands.

Fig. S18. Bayesian inference phylogenetic tree of *Cathaica* species from Shandong based on a concatenated dataset of partial 16S (A) and ITS2 sequences (B). The trees are rooted on the outgroup *Camaena cicatricosa*. Bayesian posterior probabilities and bootstrap values are given in the following order: BI/ML/MP. BI posterior probabilities lower than 0.70 and ML/MP bootstrap values lower than 50% are not shown. For the MP tree based on 16S, CI = 0.631, RI = 0.850, TL = 325. For the MP tree based on 16S, CI = 0.631, RI = 0.850, TL = 325. For the MP tree based on ITS2, CI = 0.919, RI = 0.953, TL = 99. Numbers at tips are specimen numbers.

Table S1. Details of specimens collected and localities.

Table S2. Specimens used in the phylogenetic analysis.

Table S3. Genetic distance of *Cathaica* s.s. based on 16S and ITS2.

Data S1. TNT files for morphological characters.

Data S2. Taxonomy of *Pliocathaica*.