## INTRODUCTION

There are approximately 70 Chinese species and subspecies in the bradybaenine genus *Cathaica* Möllendorff, 1884 (Gredler 1878; Gredler 1882; Tryon 1887; Moellendorff, 1899; Andreae, 1900; Gude 1902a; Gude 1902b; Yen, 1935; Yen 1939; Zilch, 1960; Zilch, 1968; Chen & Zhang, 2004). *Pseudiberus* Ancey, 1887 was included as a subgenus in *Cathaica* by Andreae (1900). However, it has been treated as distinct from *Cathaica* by some authors (Pilsbry, 1895; Möllendorff, 1899; Richardson, 1983; Zhang et al. 2021). In addition, Andreae (1900) described four additional subgenera in *Cathaica,* namely *Eucathaica* (=*Cathaica*)*, Pliocathaica, Xerocathaica* and *Campylocathaica*. Gude (1902) followed Andreae (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 Andreae (1900), but 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 subgenera level is sometimes raised to genera 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 Andreae (1900) Richardson (1983) and Chen & Zhang (2004) (see Table

1). *Cathaica* s. str. 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 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. pyrrhozona,* 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. str. mainly inhabit the provinces of Shandong, Henan and Hebei (Yen, 1939; Ping, 1929; Pilsbry,1931). 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 str. Two common members, *Cathaica pyrrhozona* (Philippi, 1845) 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 4 attributed to *Campylocathaica* (Andreae, 1900; Thiele, 1931). Overall, species of the genus *Cathaica* inhabit arid or semiarid 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 *Trichobradybaena*. According to Wu (2004, 2019), *Pliocathaica* is the sister group of *Karaftohelix*. *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, China.

## 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, Supplementary Table 1). All specimens of *Cathaica* obtained in this study, *Cathaica fasciola*, *C. pyrrhozona*, *C. leei*, *C. fohuiensis*, *C. multicostata*, *C.* sp1 and *C.* sp2, were from the subgenus *Cathaica* (*Cathaica* s.str). 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, Piocathaica* *gansuica, and Pseudiberus* specimens were obtained from Shandong Province, Anhui Province, Henan Province, Hebei Province, Shaaxi Province and Gansu Province (Supplementary Table 1). Live adult snails were relaxed in 5% ethanol for 6 hours 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 are 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 the 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 carina on penultimate whorl; LM3, the right terminal point at carina on the whorl before the penultimate whorl; LM4, apex (embryonic shell); LM5, the left terminal point at carina on the whorl before penultimate whorl; LM6, the left terminal point at carina on body whorl; LM7, the intersection of peristome and contour of body whorl; LM8, the end of carina on body whorl/peristome; LMs 9–36, semi-landmarks on the outline between LM6 and LM7 by length, LMs 37–72, semi-landmarks on the contour of the aperture by length, from LM1 via LM 8 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 Canononical 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. *C. multicostata* 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. PCA and CVA analyses were not undertaken for *Pliocathaica* members as *Pliocathaica* species can be readily distinguished by their shells.

## DNA Extraction, PCR and Sequencing

Whole DNA was extracted from a 1 mm$^3$ piece of pedal muscle using either the Tiangen DP316 kit following manufacturer's instructions or CTAB method

(Goodacre and Wade, 2001). An approximately 450bp section of the mitochondrial 16S rRNA gene and an approximately 750bp section of the ITS2 marker were amplified using polymerase chain reaction (PCR). Each 25 μl PCR mix consisted of 12.5 μl cwbio 2× Es Taq MasterMix Dye or Bioline Taq MasterMix, 9.5 μl $ddH_2O$, 1 μl 10μM forward primer, 1 μl 10 μM reverse primer and 1 μl 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 $^{o}$C for pre-denaturing followed by 40 cycles of 10 s at 94 $^{o}$C, 50 s at 45 $^{o}$C and 50 s at 72 $^{o}$C, and a final extension at 72 $^{o}$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 $^{o}$C for pre-denaturing, 30 cycles of 30 s at 94 $^{o}$C, 30 s at 50 $^{o}$C and 90 s at 72 $^{o}$C, and a final extension at 72 $^{o}$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. 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). 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 2 runs for 4,000,000 generations sampling every 2,000 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 10 random plus 10 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 1,000 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 Supplementary Table 2.

## 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) and Wu (2009). Morphological characters were scored and written in TNT format (Goloboff, 2022), see Supplementary File 1 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 lead to (0) dart sac chamber, (1) dart chamber, (2) atrium; **char3:** Entrance of mucous glands lead to (0) dart sac chamber, (1) dart chamber, (2) accessory sac chamber; **char4:** Mucous glands (0) not tightly, (1) tightly; **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.

## Taxonomic level delimitation analysis

Taxonomic level delimitation tests were performed using ASAP (Puillandre et al., 2020) and mPTP 0.2.4 (Kapli et al., 2017). For ASAP analysis, p-distances calculated by MEGA 11 were used. For mPTP analysis, Bayesian inference 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: 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—mollusk 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. str. species mostly from Shandong Province, but with some samples from Anhui Province and Gansu Province. Additionally, we examined 166 specimens of *Pliocathaica* from Shandong Province, Anhui Province, Henan Province, Hebei Province, Shanaxi Province, and Gansu Province, China.

### Morphological Analysis

Examination of the shell (Fig 3) showed that *Cathaica fasciola* and *C. pyrrhozona* 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 tightly) before entering the dart sac. *Cathaica fasciola* (Draparnaud, 1801) belongs to 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 pyrrhozona* (Philipi, 1847) and *C. leei* Yen, 1935 belong to 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, n. sp. belongs to 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, n. sp. belongs to this arrangement (Fig 4D).

Each *Cathaica* s. str. species has distinct morphological characters of the genital system or shells. *Cathaica fasciola* have two proximal accessory sacs, one on each side of the dart sac (Fig 4A). *Cathaica fohuiensis* n. sp., *C. multicostata* n. sp., *C. leei* and *C. pyrrhozona* each have a single proximal accessory sac on the right side of the dart sac (Fig 4B–D). In *C. fohuiensis* n. sp., the base of the vagina is enlarged when compared to *C. pyrrhozona* and *C. leei*, (Fig 4C). *Cathaica multicostata* is significantly different from other *Cathaica* s. str. 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, which is lower than in other *Cathaica* s. str. species from Shandong.

In species attributed to *Pliocathaica*, two arrangements of the genital system can be recognised (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) belongs to 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) belongs to 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. str. In *Cathaica s. str*. the proximal accessory sac is on the right side of the dart sac except *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 *P. gansuica* which doesn't have a proximal accessory sac. *Pliocathaica buvigneri* are 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 *P. buvigneri*.

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

In the scatter plots of PCA scores based on landmarks and semi-landmarks from apertural views of *Cathaica* s. str. species from Shandong, PC1 explains 36.925% and PC2 explains 31.319% of the total shape variation of shells (Fig 5A). *Cathaica pyrrhozona* exhibits significant variation and cannot be distinguished from the other *Cathaica* s. str. 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. str. species from Shandong. CV1 explains 72.192% and CV2 explains 20.4% of the total shape variation of shells (Fig 5B). CVA analysis 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

*Cathaica fasciola* and *C. pyrrhozona C. leei* formed well individualized clusters. However, *Cathaica fohuiensis* did not and clustered with either *C. fasciola* or *C. pyrrhozona*.

## Molecular phylogenetic analyses

The phylogenetic tree of species attributed to *Cathaica* and *Pliocathaica* from Shandong based on Bayesian inference is shown in Fig. 6. *Camaena cicatricosa* was used as the outgroup to root the phylogenetic tree and the tree also includes *Pseudiberus*, *Euhadra* and *Bradybaena*. BI, ML and MP trees have highly consistent topologies. *Cathaica* s. str. is monophyletic with representatives of *Cathaica* s. str. clustering together in the tree with relatively strong support (PP=1.00 BI, 64% ML, 99% MP). However, *Pliocathaica* is not monophyletic with representatives of the subgenus *Pliocathaica* falling separately between other genera, such as *Pseudiberus and Euhadra*. Two main nodes are robustly supported in the tree, one is *Cathaica* s. str. plus *P. buvigneri* (PP = 1.00 BI, 85 % ML and 69 % MP bootstraps), the other is *Pliocathaica pulveratricula and P. gansuica* together with *Pseudiberus zenonis* and *Euhadra stictotaenia* (PP = 1.00 BI, 91% ML, 91% and MP bootstraps). These two groups form sister groups in the tree, with *Bradybaena brevispira* falling immediately outside of this grouping.

Each species attributed to *Cathaica* s. str. forms its own branch in all trees produced with different analytical methods. The widespread species *Cathaica 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. str. 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 ML and MP (BI=0.96, ML=86%, MP is 71%). *C. multicostata* n. sp 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. str species. (PP=1.00 BI, 64% ML, 99% MP). *Pliocathaica buvigneri* is monophyletic with full support (PP=1.00 BI, 100% ML, 100% MP) and forms the sister clade of *Cathaica* s. str. 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 value=1.059190e-02), the *Cathaica* s. str. species complex is delimited into 8 groups corresponding to *Cathaica fasciola*, *C. pyrrhozona*, *C. leei*, *C. multicostata*, *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 *Cathaica fohuiensis* n. sp. into two groups. The *Pliocathaica* species are delimited into 3 groups corresponding to *Pliocathaica buvigneri*, *P. gansuica* and *P. pulveratricula*. We note that the second lowest ASAP result (ASAP score 2.0, p value=4.071856e-01) matches our results perfectly with *Cathaica* s. str. split into 7 groups comprising *Cathaica fasciola*, *C. pyrrhozona*, *C. leei*, *C. multicostata*, *C. fohuiensis*, *C.* sp1 and *C.* sp2 and with the *Pliocathaica* species split into 3 groups comprising *Pliocathaica buvigneri*, *P. gansuica* and *P. pulveratricula*. The genetic distances used by ASAP are shown in Supplementary Table 3.

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

## Character mapping

The morphological characters are shown mapped onto the phylogenetic tree in Fig. 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 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; Supplementary Figure 17C) 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 (Figs 4A–D) is an apomorphic character of *Cathaica*. The basal expanded vagina (Fig. 4C) is the apomorphic character for *Cathaica fohuiensis*.

Homoplastic characters, distribute at both genera level and species level.

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 (Figs 4B–E) is a homoplastic character for *Pliocathaica buvigneribuvigneri* and *Cathaica*. Likewise, the entrance(s) of mucous glands leading to the dart sac chamber (Figs 4A–D) is a homoplastic character for *Cathaica* and the double proximal accessory sac (Figs 4A) is a homoplastic character for *Cathaica fasciola*.

## DISCUSSION

*Cathaica* was subdivided into four subgenera by Andraea (1900) based on thick (*Pliocathaica*) or thin (*Xerocathaica*, *Campylocathaica*, *Cathaica* s. str.) shells, absence (*Cathaica* s. str., *Pliocathaica*) or presence (part of *Xerocathaica*, *Campylocathaica*) of keel, narrow (*Pliocathaica*) or comparatively wide (*Cathaica* s. str., *Xerocathaica*, *Campylocathaica*) umbilicus, reflected (*Pliocathaica*, *Campylocathaica*) or un-reflected (*Cathaica* s. str., *Xerocathaica*) aperture, and absence (*Xerocathaica*, *Campylocathaica*) or presence (*Cathaica* s. str., *Pliocathaica*) of 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. str. is monophyletic in our phylogenetic tree, *Pliocathaica* is not monophyletic in our tree and is thus not supported as a distinct genus. Instead, *Pliocathaica* is split into 3 groups; *Pliocathaica buvigneribuvigneri* is the sister group of *Cathaica* s. str. and *Pliocathaica pulveratricula and P.*

*gansuica* cluster with *Pseudiberus* and *Euhadra* (Fig 6). According to previous treatments, e. g. Gude (1902a), *Pliocathaica buvigneribuvigneri*, *P. pulveratricula* and *P. 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. str. instead of *Cathaica* s. str. plus *Pliocathaica buvigneribuvigneri*, it suggests that *Pliocathaica buvigneri* should not belong to *Cathaica* s. str.

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

Previously, *C. pyrrhozona* has been treated either as a subspecies or a synonym of *C. fasciola* (Chen & Zhang, 2004; Suzuki, 1939) since no differences in shell morphology have been identified. The systematic significance of differences in the reproductive anatomy of *C. pyrrhozona and C. fasciola* has not been recognised. However, *Cathaica fasciola* has been considered to be widely distributed (Pilsbry, 1894; Möllendorff, 1899; Andreae, 1900; Chen & Zhang, 2004). However, Geometric Morphometric (GM) results showed that *C. pyrrhozona* has more variable shells. Other than one specimen of *C. fasciola*, specimens collected from Shandong were *C. pyrrhozona.* 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 *Cathaica pyrrhozona* and *Cathaica fasciola* are sister groups sharing similar conchological characteristics, however, *C. pyrrhozona* has a single proximal accessory sac and *C. fasciola* has double proximal accessory sacs. Considering the situation of type specimens, we designated neotype for *Cathaica pyrrhozona* to make the taxonomic position clear.

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

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

In the newly described species *Cathaica 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. str. 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. str. with a wide umbilicus, almost horizontal apex, and sparse ribs on the thin shell, 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 genital system variation checks. *Cathaica* sp1 forms the sister group of *C. leei* in the phylogenetic tree. *C.* sp2 is the sister group of *C*. *fohuiensis*.

*Cathaica pyrrhozona* is widely distributed in Shandong, especially in cities and other anthropogenic environments; *C. leei* occurs on higher altitudes of Mount Tai (usually above 800 m above sea level (a. s. l.)) *C. fohuiensis* occurs above 340 m a. s. l. on Fohui Mountain (adjacent to the Mount Tai). *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. str. *Pliocathaica buvigneri* and *P. pulveratricula*, differ from

*Cathaica* s. str. in the direction of the proximal accessory sac and in where the sac enters the vagina. *Pliocathaica gansuica* can be distinguished from *Cathaica* s. str.as it has an accessory sac instead of a proximal accessory sac, shorter penial sheath and epiphallic papilla (Wu, 2004)

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

In *P. pulveratricula* the penial pilasters are similar to those of *Pseudiberus* and not parallel as with other *Cathaica* s. str. members and the penial tissue is more delicate than that of *P. 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*, *P. 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. str 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 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* s. str). Here, we use three informal names to represent these three genera-level taxa, aff. *Pliocathaica*, for *P. pulveratricula,* Richthofeni-A (Richthofeni group from Andreae 1900) for *Pliocathaica buvigneri* and Richthofeni-B for *P. gansuica*..

Previously, the presence and 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 genera level taxa (*Bradybaena*, *Euhadra*, *Pseudiberus*, *Cathaica*, aff. *Pliocathaica*, Richthofeni-A and Richthofeni-B), gain and loss of genital characteristics are only discovered between genera and not between species. This hypothesis matches the hypothesis of genital system evolution at the genera level proved by the results from Beese et al. (2009) and Wu (2004, 2019). Based on studied genera 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 checking. The proximal accessory sac is a special organ; *Cathaica fasciola* gain 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 genera 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 evolved among species in one genus. The evolution of genital characteristics among species in one genus is probably caused by environmental pressure. For example, *Cathaica fasciola* has double proximal accessory sacs.

## Systematic account of *Cathaica* s. str.

### 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, *Cathaica fasciola* lacks the poly-layered structure (PLs) 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 neotype is designated in material examined section of *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. Museum material: NHMUK 1912.6.27.45; SMF22861a; NHMUK 1921.10.6.48–50. Other material: Woyang, Bozhou, Anhui Province, fifteen 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 with irregular thickenings. Young shell rough, angulated. Adult shell smooth. Teleoconch without microscopic structure. Adult body whorl rounded at periphery or slightly bluntly angulate supraperipherily. 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 9 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, *Cathaica 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 *Cathaica fasciola* and the other *Cathaica* spp. mentioned in this paper there is not true accessory sac. In the phylogenetic analysis, this species is the sister group of *Cathaica 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 slightly keel presents 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, fig. 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 nos 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, eleven 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; Menya 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 HBUMM 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 with 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. Epiphallic papilla absent. Flagellum lacking. Vas deferens thickened near penial retractor. Mucous glands approximate 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:* Based on divergent features ranging from shell morphology, the genital system and molecular evidence (Figs 3A–C, 4–6), we present robust evidence that *Cathaica fasciola* and *C. pyrrhozona* are distinct species In the basic illustration of the genitalia of '*Eulota pyrrhozona'* 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, n. sp., which shares the expanded proximal vagina shown in Pilsbry's figure.

The shells of *C. pyrrhozona* vary greatly among different geographic populations and are difficult to be distinguished from those of C. *fasciola*. Generally, the periphery of *C. pyrrhozona* 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

The type specimens of *Cathaica pyrrhozona* could not be located (Kabat & Coan, 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), so a neotype was designated based on Article 75 of the International Code of Zoological Nomenclature. The reasons are the following. Without a neotype, it is impossible to confirm which species is currently designated as *Cathaica pyrrhozona*. This is because *Cathaica pyrrhozona* cannot be distinguished from *Catahica fasciola* on conchological characters, and no soft body was described when either species was originally described. Additionally, *Cathaica pyrrhozona* has not been located in Wusong, Shanghai (South China), the locality based on the original literature. This is significant because *Cathaica pyrrhozona* (or *Cathaica pyrrhozona* shaped species) is widely distributed in North China, and there is only a plain between Shandong (North China) and Shanghai, which *Cathaica pyrrhozona* could easily have spread across. Therefore, the secure stability of the nomenclature for *Cathaica pyrrhozona* cannot be confirmed without designing a neotype

### ***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 vouncher nos. 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 with 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 iyellowish 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 over 800 m a.s.l. They were observed active on the 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.), examples are mixed with *C. leei* in the molecular analysis (Fig.5).

## ***Cathaica multicostata* Zhang, n. sp.**

(Figs 1, 3E, 4D, 5–6)

*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 $^{O}$N, 117.721°E, 520 m a s. l.; April 30, 2018; Coll. GZ, Y. Zhang, D. Li. Paratypes: 2 FMA, SDNU.Gas.0194.01.01–SDNU.Gas.0194.01.02; Baodu, Zaozhuang, Shandong; 34.983 $^{O}$N, 117.714 $^{O}$E, 340 m a. s. l.; April 30, 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 supraperipharily 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; 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 (Andraea, 1900) *C. multicostata* Zhang, n. sp. 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*. The shells of species are similar to *Cathaica mengi* Yen, 1935 occurring in South Shanxi Province but can be distinguished with *C. mengi* with thin flat shell, absence of basal tooth, stronger and sparse ribs, (Zhang et al. 2020).

### *Cathaica fohuiensis* Zhang, n. sp.

(Figs 1, 3F, 4C, 5–6)

*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 with irregular thickenings. Young shell rough, angulated. Adult shell smooth. Teleoconch without other microscopic structure. Adult body whorl rounded at periphery or slightly bluntly angulate supraperipherily. 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 higher spiral whorl (Fig. 5), but the base of vagina is expanded (Fig. 3C) and this character is apomorphic character for *Cathaica* s. str.

## DATA AVAILABILITY

The gene sequences are available on the GenBank Nucleotide Database at: https://www.ncbi.nlm.nih.gov/genbank/ and can be accessed with the access numbers shown in the Supporting Information.

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## REFERENCES

Ancey CF. 1882. Coquilles nouvelles ou peu connues. *Le Naturaliste* 4: 119.

Ancey CF. 1883. Les mollusques des parties centrales de l'Asie (Chine et Thibet) récoltés par Mr. l'abbé A. David. *Il naturalista siciliano organo della Società siciliana di scienze naturali* 2 (7): 163–168.

Andreae A. 1900. Land-und Süsswasserschnecken aus Zentral und Ostasien. *Durch Asien* 3: 43–89.

Beese K, Armbruster GFJ, Beier K, Baur B. 2009. Evolution of female sperm-storage organs in the carrefour of stylommatophoran gastropods. *Journal of Zoological Systematics and Evolutionary Research* 47: 49–60.

Blume W. 1925. Die Konchylien der Stoetznerschen Szetschwan-Expedition. *Archiv für Molluskenkunde* 57: 9–22.

Castresana J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* 17: 540–552.

Chen D, Gao J, Gao F. 1990. Snail fossil combination in the loess stratum of Shandong Peninsula and its significance. *Proceedings of the Second Meeting of the Chinese Zoological Society and the Third Academic Symposium of the Chinese Society of Zoology*: 156–163.

Chen D, Zhang G. 1987. *Chinese Economy Fauna, Terrestrial Mollusc*. Beijing: Science Press, 186 pp.

Chen D, Zhang G. 2004. *Fauna Sinica, Invertebrata vol. 37, Bradybaenidae*. Beijing: Science Press, 482 pp, 8 pls.

Coan EV, Kabat AR. 2017. The malacological contributions of Rudolph Amandus Philippi (1808–1904). *Malacologia* 60: 31–322.

Darriba D, Posada D, Kozlov MA, Stamatakis A, Morel B, Flouri T. (2020) ModelTest-NG: A new and scalable tool for the selection of DNA and protein evolutionary models. *Molecular Biology and Evolution* 37: 291–294.

Debeaux O. 1868. Notice sur la malacologie de quelques points du littoral de l' empire chinois. *Journal de Conchyliologie* 11: 239–252.

Deshayes GP. 1870. Diagnoses d'espèces nouvelles de mollusques terrestres et fluviatiles de la principauté de Moupin, Thibet oriental, envoyées au muséum d'histoire naturelle de Paris par M. l'abbé Armand David, missionaire. *Nouvelles Archives du Muséum d'Histoire Naturelle* 6: 19–27.

Deshayes GP. 1873. Diagnoses d'espèces nouvelles de mollusques terrestres et fluviatiles de la principauté de Moupin, Thibet oriental, envoyées au muséum d'histoire naturelle de Paris par M. l'abbé Armand David, missionaire. *Nouvelles Archives du Muséum d'Histoire Naturelle* 9: 3–14.

Deshayes GP. 1874. Diagnoses d'espèces nouvelles de mollusques terrestres et fluviatiles de la principauté de Moupin, Thibet oriental, envoyées au muséum d'histoire naturelle de Paris par M. l'abbé Armand David, missionaire. *Nouvelles Archives du Muséum d'Histoire Naturelle* 10: 83–97.

Draparnaud JPR. 1801. *Histoire naturelle des Mollusques terrestres et fluviatiles de la France*. Paris, 164 pp, 13 pls.

Goloboff PA, Catalano SA. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32: 221–238.

Goloboff PA, Torres A, Arias JS. 2017. Weighted parsimony outperforms other methods of phylogenetic inference under models appropriate for morphology. *Cladistics* 34: 407–437.

Goloboff PA. 2022. *Phylogenetic Analysis of Morphological Data: From Observations to Optimal Phylogenetic Trees*. Boca Raton: CRC Press, 277pp.

Goodacre SL, Wade CM. 2001. Molecular evolutionary relationships between partulid land snails of the Pacific. *Biological Sciences* 268: 1–7.

Gredler PV. 1878. Zur Conchylien-Fauna von China I. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* 10: 101–105.

Gredler PV. 1882. Zur Conchylienfauna von China IV. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft* 9: 38–50.

Gredler PV. 1887. Zur Conchylien-Fauna von China X. *Malakozoologische Blätter* 9: 121–163.

Gude GK. 1902a. A classified list of the helicoid land shells of Asia. *Journal of Malacology* 9: 1–11.

Gude GK. 1902b. A classified list of the helicoid land shells of Asia. *Journal of Malacology* 9: 51–59.

Heude PM. 1882–1890. *Mémoires concernant l'histoire naturelle de l'empire chinois par des pères de la Compagnie de Jésus. Notes sur les Mollusques terrestres de la vallée du Fleuve Bleu*. Chang-Hai: Mission Catholique, 188 pp.

Hilber von V. 1882. Recente und im Löss gefundene Landschnecken aus China. *Sitzungsberichte der Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse* 86: 313–352.

Hirano T, Kameda Y, Kimura K, Chiba S. 2014. Substantial incongruence among the morphology, taxonomy, and molecular phylogeny of the land snails *Aegista*, *Landouria*, *Trishoplita*, and *Pseudobuliminus* (Pulmonata: Bradybaenidae) occurring in East Asia. *Molecular Phylogenetics and Evolution* 70: 171–181.

Kapli P, Lutteropp S, Zhang J, Kobert K, Pavlidis P, Stamatakis A, Flouri T. 2017. Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. *Bioinformatics* 33: 1630–1638.

Kerney MP, Cameron RAD. 1979. *A field guide to the land snails of Britain and north-west Europe*. London: Collins Press, 288pp.

Klingenberg CP. 2011. MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources* 11: 353–357.

Kobelt W. 1897. *Die Schnirkelschnecken nebst den zunächst verwandten Gattungen. Vierter Theil. In: Küster, H. C.; Kobelt, W., Eds. Systematisches Conchylien-Cabinet von Martini und Chemnitz. Neu herausgegeben und vervollständigt. Ersten Bandes, zwölfte Abtheilung*. Nürnberg: Bauer & Raspe, 525–859 pp, 162–228 pls.

Kozlov AM, Darriba D, Flouri T, Morel B, Stamatakis A. 2019. RAxML-NG: a fast, scalable and user-friendly tool for Maximum Likelihood phylogenetic inference. *Bioinformatics* 35: 4453–4455.

Köhler F, Criscione F. 2013. Small snails in a big place: a radiation in the semi-arid rangelands in northern Australia (Eupulmonata, Camaenidae, *Nanotrachia* gen. nov.). *Zoological Journal of the Linnean Society* 169: 103–123.

Martens EV. 1873. Neue Helix-Arten aus China. *Malakozoologische Blätter* 21: 67–

69.

Martens EV. 1882. Über centralasiatische Mollusken. *Mémoires de l'Académie impériale des Sciences de St.-Pétersbourg, Classe physico- mathématique* 30: 1–65.

Möllendorff von OF. 1875. Landschnecken der nordchinesischen Provinz Chili. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft* 2: 214–220.

Möllendorff von OF. 1881. Zur Binnenmolluskenfauna von Nordchina. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft* 8: 33–43.

Möllendorff von OF. 1884. Materialien zur Fauna von China. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft* 11: 307–390.

Möllendorff von OF. 1899. Binnen-Mollusken aus Westchina und Centralasien I. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Petersbourg*, 144 pp, 8 pls.

Möllendorff von OF. 1901. Binnen-Mollusken aus Westchina und Centralasien II. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Petersbourg*, 113 pp, 6 pls.

Nakamura T, Yamada KD, Tomii K, Katoh K. 2018. Parallelization of MAFFT for large-scale multiple sequence alignments. *Bioinformatics* 34: 2490–2492.

Nixon KC. 2021. WinClada, version 2.0. New York: Willi Hennig Society.

Pfeiffer L. 1860. *Die Schnirkelschnecken nebst den zunächst verwandten Gattungen. Dritter Theil. In: Küster, H. C., Ed. Systematisches Conchylien-Cabinet von Martini und Chemnitz. Neu herausgegeben und vervollständigt. Ersten Bandes, zwölfte Abtheilung*. Nürnberg: Bauer und Raspe, 291–524 pp.

Philippi L. 1847. Ueber die Eintheilung der Cyclostomaceen. *Zeitschrift für Malakozoologie* 4: 45–48.

Pilsbry HA. 1892. *Manual of conchology, structural and systematic: with illustrations of the species, 2 (8)*. Philadelphia: Conchological Section, Academy of Natural sciences of Philadelphia, 314 pp, 58 pls.

Pilsbry HA. 1894. *Manual of conchology, structural and systematic: with illustrations of the species, 2 (9)*. Philadelphia: Conchological Section, Academy of Natural sciences of Philadelphia, 366 pp, 71 pls.

Ping C. 1929. Fossil terrestrial gastropods from north China. *Palaeontologia Sinica, Series B* 6: 5–29.

Ping C. 1931. Tertiary and Quaternary non-marine gastropods of north China. *Palaeontologia Sinica, Series B* 6: 16–20.

Puillandre N, Brouillet S, Achaz G. 2020. ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources* 21: 609–620.

Richardson L. 1983. Bradybaenidae: catalog of species. *Tryonia* 9: 1–253.

Ridley M. 1989. The cladistic solution to the species problem. *Biology and Philosophy* 4: 1–16.

Rohlf FJ. 2004a. TpsUtil. Department of Ecology and Evolution, State University of New York, Stony Brook, NY.

Rohlf FJ. 2004b. TpsDig. Department of Ecology and Evolution, State University of New York, Stony Brook, NY.

Ronquist F, Teslenko M, Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic Biology*, 61(3): 539–542.

Schileyko AA. 2004. Treatise on recent terrestrial pulmonate molluscs. Part 12. Bradybaenidae, Xanthonychidae, Epiphragmophoridae, Helminthoglyptidae, Elonidae, Sphincterochilidae, Cochlicellidae. *Ruthenica* Supplement 2: 1627–1763.

Sturany R. 1900. 1900 W. A. Oberutschews Mollusken Ausbeute aus Hochasien. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 70: 17–48.

Suzuki K. 1939. Materials to the knowledge of the Cenozoic non-marine Mollusca of north China I. *Journal of the Geological Society of Japan* 46: 91–122.

Swindell SR, Plasterer, TN. 1997. SEQMAN. Contig assembly. *Methods in Molecular Biology* 70: 75–89.

Tamura K, Stecher G, Kumar S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis Version 11, *Molecular Biology and Evolution* 38: 3022–3027.

Thiele J. 1931. *Handbuch der systematischen Weichtierkunde*. Jena (Fischer). (2): 377–778.

Tryon GW. 1887. *Manual of conchology, structural and systematic: with illustrations of the species. 2 (3)*. Philadelphia: Academy of Natural Sciences of Philadelphia, 313 pp, 63 pls.

Vaidya G, Lohman DJ, Meier R. 2011. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information.

*Cladistics* 27: 171–180.

Vinarski MV, Eschner A. 2016. Examination of the type material of freshwater mollusk species described by J.P.R. Draparnaud. *Annalen des Naturhistorischen Museums in Wien B* 118: 29–53.

Wade CM, Hudelot C, Davison A, Naggs F, Mordan PB. 2007. Molecular phylogeny of the helicoid land snails (Pulmonata: Stylommatophora: Helicoidea), with special emphasis on the Camaenidae. *Journal of Molluscan Studies* 73: 411–415.

Wang H, Chen D. 2011. *Terrestrial malacology in Chinese important areas*. Lanzhou: Gansu Science and Technology Press, 527 pp.

Wiegmann F. 1900. Binnen-Mollusken aus Westchina und Centralasien. *Annuaire du Musee Zoologique de l'Academie Imperiale des St.-Petersburg* 5: 1–186

Wu M, Qi G. 2004. A taxonomic note on *Pseudiberus* Ancey, 1887 (Gastropoda: Pulmonata: Bradybaenidae). *Folia Malacologica* 14: 25–30.

Wu M. 2004. Preliminary phylogenetic study of Bradybaenidae (Gastropoda: Stylommatophora: Helicoidea). *Malacologia* 46: 79–125.

Wu M. 2019. a Taxonomic Note on the Helicoid Land Snail Genus Traumatophora (Eupulmonata, Camaenidae). *Zookeys* 835: 139–152.

Yen TC. 1935. The non-marine gastropods of north China. Part I. *Publications du Musie Hoangho Paiho de Tien Tsin* 34: 1–57, 5 pls.

Yen TC. 1939. Die chinesischen Land-und Süsswasser-Gastropoden des Natur-Museums Senckenberg. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaf* 444: 131–156.

Yen TC. 1941. Malacological research and its future advancement in China. *The Asiatic Review* 37: 124–133.

Yen TC. 1942. A review of Chinese gastropods in the British Museum. *Proceedings of the Malacological Society of London* 24: 170–289.

Zhang G, Ge L, Hao S, Liu T. 2020. Current Status and Illustrations of the Type Specimens of the Species Described by Teng-Chien Yen in 1935 belonging to *Cathaica* Möllendorff, 1884 and *Pseudiberus* Ancey, 1887 (Gastropoda, Pulmonata, Camaenidae). *Archiv für Molluskenkunde* 149: 55–65.

Zhang D, Wu N-Q, Li F-J, Rousseau D-D, Chen X-Y, Dong Y-J, Lu H-Y. 2021. Climatic structures and intensities of the last two glacials documented by terrestrial Molluscs from Chinese loess sequences. *Boreas* 50: 308–320.

Zhang G, Wu M, Köhler F, Liu T. 2021. Review of the Genus *Pseudiberus* Ancey, 1887 (Eupulmonata: Camaenidae) in Shandong Province, China. *Malacologia* 63: 257–284.

Zhang J, Kapli P, Pavlidis P, Stamatakis A. 2013. A general species delimitation method with applications to phylogenetic placements. *Bioinformatics* 29: 2869–2876.

Zilch A. 1951. Zur Nomenklatur einiger Landschnecken aus China. *Archiv für Molluskenkunde* 80: 86.

Zilch A. 1960. *Gastropoda. Teil 2. Euthyneura. In: Schindewolf, OH, eds, Handbuch der Paläozoologie*. Berlin: Borntraeger, 401–600 pp.

Zilch A. 1968. Die Typen und Typoide des Natur-Museums Senckenberg. 41: Mollusca, Bradybaenidae, Bradybaeninae. *Archiv für Molluskenkunde* 98: 155–212.