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Disentangling the *Pelodiscus axenaria* complex, with the description of a new Chinese species and neotype designation for *P. axenaria* (Zhou, Zhang & Fang, 1991)

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Abstract

We describe a new species from the *Pelodiscus axenaria* complex from Hunan and Jiangxi Provinces, China. Also, the application of the name *P. axenaria* (Zhou, Zhang & Fang, 1991) is clarified by designating a neotype for this species. Besides its genetic divergence, the new species differs from all other *Pelodiscus* species, including the two other taxa constituting the complex (*P. axenaria*, *P. huangshanensis*), in the following combination of morphological traits: (1) small adult size, <15 cm carapace length; (2) carapace distinctly keeled, more or less strongly tuberculated, usually olive clay-coloured and adorned with greenish black marbling; (3) plastron yellowish white, typically immaculate except for a blurred-edged blotch behind each axilla that does not extend to the entoplastron and some slight black suffusion along its anterior border; (4) underside of the leathery margin of the carapace with varying amounts of dark pigmentation; (5) head olive clay-coloured with numerous black splotches; (6) chin grey brown with pale stipples, throat dark grey, finely spotted with black; (7) neck with a wide yellow lateral band stretching from the tympanum posteriorly, which tends to fade with age; (8) entoplastron boomerang-shaped, the amount of bending of the transverse bar between the two posteriolaterally directed rami >90°.

Key words: China, genetics, morphology, Pelodiscus shipian sp. nov., phylogeny, soft-shelled turtle, taxonomy

Introduction

The binomen *Trionyx axenaria* was first proposed by Zhou *et al.* (1991) in the English abstract of a Chinese-language paper dealing with soft-shelled turtles called by the local populace 砂鳖 (sha bie = sand soft-shelled turtle) inhabiting rivers in the following counties and cities of Hunan Province, China: Taoyuan, Pingjiang, Rucheng, Lingling, and Shaoyang. Even though the diagnostic morphological features of 'sha bie' remain unclear to date, molecular genetic studies (Chen *et al.* 2005, 2006; Dong *et al.* 2016; Fritz *et al.* 2010; Gong *et al.* 2018; Yang *et al.* 2011) have confirmed the distinctiveness of the sand soft-shelled turtle, and it has been treated as a valid species of the genus *Pelodiscus* in all major turtle taxonomy checklists published after 2007 (Fritz & Havaš 2007; Rhodin *et al.* 2008; TTWG 2007, 2009, 2010, 2011, 2012, 2014, 2017, 2021).

Two recent studies employing nuclear and mitochondrial DNA sequences revealed that *P. axenaria* belongs to a species complex comprising three morphologically challenging lineages (Gong *et al.* 2018, 2021). One of these lineages was recently described as *Pelodiscus huangshanensis* Gong, Peng, Huang, Lin, Huang, Xu, Yang & Nie, 2021, whereas another lineage discovered by Gong *et al.* (2018) still needs to be formally named. This 'lineage I' differs both in nuclear and mitochondrial DNA sequences from all other *Pelodiscus* species and is, according to current understanding, the sister species of *P. huangshanensis* (Gong *et al.* 2018, 2021).

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However, the identity of *P. axenaria* is obscure, rendering the present classification preliminary. The original description of *P. axenaria* (Zhou *et al.* 1991) makes no mention of any type material or its place of deposition; their tables list data from 73 "randomly selected" sand soft-shelled turtles, none of which is individually recognizable. These specimens constitute syntypes (ICZN 1999: Article 72.1.1) but cannot be located. In the collection of Gongjian Zhou's home institution, the Hunan Normal University, Changsha, there are no specimens that can be identified with the type material of *P. axenaria* (Xiang Xu and Shuqiang Li, *in litt.* 14 February 2020; TTWG 2021; Iverson 2022). Also, a later mention of a specimen in the collection of the Hunan Normal University (HNNU1991001ZGJ) as the holotype of *P. axenaria* by other authors (Zhou & Li 2013) was erroneous and, according to the International Code of Zoological Nomenclature (ICZN 1999: Article 72), invalid because no holotype was designated in the original description (Zhou *et al.* 1991).

After the discovery of two additional species in the *P. axenaria* complex (Gong *et al.* 2018, 2021), it becomes evident that the original description (Zhou *et al.* 1991) of *P. axenaria* does not resolve its taxonomic identity. Figures 1 and 2 in Zhou *et al.* (1991), meant to show the dorsal and ventral aspects of a live 'sha bie' individual, do not allow morphological recognition of *P. axenaria* compared to the morphologically very similar 'lineage I' of Gong *et al.* (2018). In the face of this taxonomic uncertainty, it is necessary to establish a standard for further comparisons by designating a neotype for *P. axenaria*. This is a continuation of our ongoing taxonomic investigations of the genus *Pelodiscus* (Fritz *et al.* 2010; Stuckas & Fritz 2011; Gong *et al.* 2018; Farkas *et al.* 2019).

Our neotype designation unambiguously allows the description of 'lineage I' as a species new to science. To do so, we genetically confirmed the identity of both the neotype of *P. axenaria* and the type material of the new species by comparing sequences of one mitochondrial gene (cyt *b*) and three nuclear loci (P26S4, R35, TB01) against the data of Gong *et al.* (2018) and Gong *et al.* (2021). Laboratory approaches for generating these DNA sequences followed Gong *et al.* (2018).

Using Bayesian inference of phylogeny as implemented in MrBayes 3.2.6 (Ronquist *et al.* 2021), the cyt *b* sequences of the new species cluster with maximal support with those of 'lineage I' of Gong *et al.* (2018), but not with their sister taxon *P. huangshanensis*, and the cyt *b* sequence of the neotype of *P. axenaria* clusters with maximal support within the sequences of this species from the dataset of Gong *et al.* (2018). Also, phased haplotypes (for description, see Gong *et al.* 2018) of the three nuclear loci cluster in exploratory haplotype network analyses using TCS (Clement *et al.* 2000) as expected for 'lineage I' (type material of the new species) or *P. axenaria* (neotype specimen), respectively. Full genetic analyses for these specimens will be presented in a forthcoming paper using additional material. For the present study, uncorrected *p* distances were calculated for the individual *Pelodiscus* species using MEGA 11 (Tamura *et al.* 2021) and the pairwise deletion option based on an alignment of 191 cyt *b* sequences from Gong *et al.* (2018, 2021), our new sequences from the type material of the new species are given below.

Measurements presented below are all straight-line and follow the standards for softshell turtles set out in Webb (1962).

Pelodiscus axenaria (Zhou, Zhang & Fang, 1991)

(Figs. 1-3)

Neotype. Jinan University, Guangzhou: JNU 20210001, adult male preserved in alcohol, Yudai River, Tongdao County, Hunan Province, China (26°09'N, 109°46'E), leg. Shiping Gong, 25 May 2021; European Nucleotide Archive (ENA) accession numbers for DNA sequences: cyt *b*—OW235725, P26S4—OW235773, R35—OW237758 and OW237759 (two alleles), TB01—OW235754 and OW235755 (two alleles).

Description of the neotype. Carapace length (CL) 128.7 mm, carapace width (CW) 113.3 mm, plastron length (PL) 88.9 mm, head width (HW) 26.8 mm, eye diameter 7.6 mm, interorbital distance 3.9 mm, snout length (SL) 12.4 mm. Carapace oval, nearly circular in appearance, slightly domed but with a clear median keel, widest at level of the posterior buttress spurs of the hypoplastra. Marginal ridge low, central tubercle indistinct. Dorsal surface smooth except for the longitudinal ridging of the bony disk and some blunt, barely discernible protuberances spread over the leathery margin, mostly confined to the pelvic region. The olive clay-coloured carapace is suffused with dark grey and black, displaying an extremely complex blotched and mottled pattern that, to some extent, resembles bilaterally symmetrical inkblots. The reticulations extend roughly from the outer (pleural) sutures of the neurals

side- and backwards to the periphery of the shell, with the two halves of the "saddle" being connected by a dark blotch, approximately at the level of neural 5. Jet black stellate spots are also present along the perimeter of the bony disk as well as the leathery margin but are not obvious due to their dark grey surroundings. The entoplastron is boomerang-shaped, the amount of bending of the transverse bar between the two posteriolaterally directed rami is >90°. Callosities are small and only present on the hyo-hypo- and xiphiplastra. Ventral surfaces are cream yellow to yellowish white, with distinct dark grey markings on both plastron and thighs. There is a blurred-edged patch between the anterior extensions of the epiplastra that breaks up into bruise-like suffusions along the anterior plastral margin and towards the entoplastron where it fades and does not contact the large central blotch covering the hyo-hypo- and xiphiplastra. There is an additional, even darker grey, fuzzy-edged blotch on both sides behind the axillae and continuing in the direction of, but not reaching, the hypplastra. Bridge and underside of leathery margin with contusion-like grey marks that are best defined along the shell borders. Fore- and hindfeet are well-webbed, having five digits each, with claws on the first three digits only. Each forelimb has four antebranchial scales, three of them free-edged. Each hindlimb has two horny scales, one smooth on the posterodorsal surface, while the other, which is free-edged, is located on the posteroventral surface. Extremities have a few scattered, very small dark spots on an olive clay-coloured background. Lower surfaces of the front legs are suffused with black, except for a patch just in front of the axillae. The inner thighs carry well-defined black markings on either side of the long and thick tail, which extends beyond the rear margin of the carapace, indicating the male gender of the specimen. Head fully extended, terminating in flexible snout. Jaws closed, each covered by fleshy lips except anteriorly where the horny beaks are exposed. Top of head with fine black specks and streaks on an olive clay-coloured ground. Pre-, sub- and postocular stripes thin and incomplete. The chin is grey brown with pale stipples, the throat dark, without any clear pattern. The lips are olive clay-coloured with light and dark flecks. There is a pale band on either side of the neck.



FIGURE 1. Dorsal and ventral aspects of the freshly dead neotype of *Pelodiscus axenaria* (JNU 20210001, adult male, 128.7 mm CL).



FIGURE 2. Neotype of *Pelodiscus axenaria* (JNU 20210001, adult male, 128.7 mm CL) in life.

Remarks. Zhou *et al.* (1991) did not provide the etymology for the species epithet '*axenaria*.' It cannot be excluded that the name originated from a typographic misspelling of the Latin adjective *arenaria* (= sandy) and had been intended as an allusion to the Chinese vernacular name of the species (砂鳖 sha bie = sand soft-shelled turtle). However, the epithet '*axenaria*' was generally accepted as a noun (of unknown meaning) in apposition, according to Article 31.1 of the International Code of Zoological Nomenclature (ICZN 1999) and we continue to do so for the sake of nomenclatural stability. Although Article 32.5 (ICZN 1999) would allow correction, we argue there is no clear evidence of an inadvertent error, especially in the light that the gender in the original combination with *Trionyx* should have been masculine ('*Trionyx axenarius*').

Pelodiscus shipian sp. nov.

(Figs. 4-6) Suggested English name: Chinese stone slab soft-shelled turtle Suggested Chinese name: 石片鳖 (shi pian bie)

Holotype. Jinan University, Guangzhou: JNU 20190011, adult female preserved in alcohol, Liaohe River, Fengxin County, Jiangxi Province, China (28°43'N, 115°25'E), leg. Shiping Gong, 18 June 2019, European Nucleotide Archive (ENA) accession numbers for DNA sequences: cyt *b*—OW235712, P26S4—OW235765, R35—OW237755.

Paratypes. Jinan University, Guangzhou: JNU 20190001–20190010, ten adult males preserved in alcohol, same data as the holotype; JNU 20190012–20190017, six adult females preserved in alcohol, same data as the holotype; JNU 20190022, four adult females preserved in alcohol, same data as the holotype; JNU 20190023, adult male preserved in alcohol, same data as the holotype; JNU 20190024, adult female preserved in alcohol, same data as the holotype; JNU 20210002, 20210003, two adult females preserved in alcohol, Shaoyang County, Hunan Province, China, leg. Shiping Gong, 7 May 2021; JNU 20210004, adult male preserved in alcohol, Taoyuan

County, Hunan Province, China, leg. Shiping Gong, 7 May 2021; JNU 20210005, adult male preserved in alcohol, Yongzhou City, Hunan Province, China, leg. Shiping Gong, 7 May 2021; JNU 20210006 adult female preserved in alcohol, Yongzhou City, Hunan Province, China, leg. Shiping Gong, 7 May 2021. ENA accession numbers of the paratypes are for cyt *b* sequences: OW235702–OW235711, OW235713–OW235724, OW235726–OW235730; for P26S4 sequences: OW235762–OW235764, OW235766–OW235772, OW235774, OW235775; for R35 sequences: OW237747–OW237754, OW237756, OW237757, OW237760–OW237762; and for TB01 sequences: OW235731–OW235753, OW235756–OW235761.

Diagnosis. Besides its genetic distinctiveness (Gong *et al.* 2018), *Pelodiscus shipian* **sp. nov.** differs from its congeners by the following combination of characters: (1) small adult size, <15 cm CL; (2) carapace distinctly keeled, more or less strongly tuberculated, usually olive clay-coloured and adorned with greenish black marbling but sometimes much darker with obscure pattern; (3) plastron yellowish white, typically immaculate except for a blurred-edged blotch behind each axilla that does not extend to the entoplastron and a slight black suffusion along its anterior border; (4) underside of the leathery margin with varying amounts of dark pigmentation; (5) head olive clay-coloured with numerous black splotches; (6) chin grey brown with pale stipples, throat dark grey, finely spotted with black; (7) neck with a wide yellow lateral band stretching from the ear backwards, which tends to fade with age; (8) entoplastron boomerang-shaped, the amount of bending of the transverse bar between the two posteriolater-ally directed rami >90°.

Pelodiscus shipian **sp. nov.** cannot be confused with any other species of *Pelodiscus* except for *P. axenaria* and, perhaps, *P. huangshanensis*, its closest relatives constituting the *P. axenaria* complex, which both have a dark chin and throat finely stippled with black or an indistinct paler colour. The remaining species (*P. maackii*, *P. parviformis*, *P. sinensis*, and *P. variegatus*) have a light grey chin and throat with white spots or larger white markings that are either or not edged with a darker colour. For additional features see Farkas *et al.* (2019: Table 4).

Pelodiscus shipian **sp. nov.** differs from *P. axenaria* by having (1) a smaller adult size of <15 cm CL (vs. >15 CL); (2) no plastral markings except, rarely, relatively small fuzzy-edged blotches behind the axillae and a slight black suffusion on the forelobe (vs. a dark grey central blotch usually present and blotches behind the axillae extending to the entoplastron); (3) usually unmarked inner thighs (vs. thighs usually carrying well-defined, rarely indistinct, black markings on either side of the tail); and (4) a head and snout with numerous black splotches but without clearly discernible pre-, sub- and postocular stripes (vs. a head with fine black specks and streaks and thin, incomplete pre-, sub- and postocular stripes).

Pelodiscus shipian **sp. nov.** differs from *P. huangshanensis* by having (1) a larger adult size of >12 cm CL (vs. <12 cm CL); (2) a rough, finely tuberculated carapace (vs. smooth carapace with tuberculation confined to the anterior edge and the leathery margin); (3) a distinctly marbled carapace pattern (vs. an olive brown to dark brown carapace without pattern); and (4) a more or less contrasting yellow lateral band on either side of the neck (vs. no lateral bands on neck when fully grown).

In the cyt *b* gene, a frequently used marker for estimating interspecific divergence in turtles (e.g., Kindler *et al.* 2012; Iverson *et al.* 2013), *P. shipian* **sp. nov.** differs from other *Pelodiscus* species on average by 5.30-7.53% (Table 1). These values resemble those as observed between species of another softshell turtle genus (*Nilssonia*; Praschag *et al.* 2007).

	n	axenaria	huangsh.	maackii parviform.		shipian	shipian sinensis	
P. axenaria	13	1.38						
P. huangshanensis	1	6.46	n/a					
P. maackii	10	8.27	7.96	0.23				
P. parviformis	28	7.59	7.49	2.45	0.11			
P. shipian	34	6.69	5.30	7.51	7.22	0.04		
P. sinensis	97	8.12	7.50	2.68	2.44	7.06	0.85	
P. variegatus	8	8.50	7.86	3.19	3.09	7.53	1.78	0.22

TABLE 1. Average uncorrected *p* distances (per cent) for *Pelodiscus* species using an alignment of cyt *b* sequences (1140 bp). On the diagonal are within-species divergences in bold.



FIGURE 3. Variation in plastron colouration and pattern in *Pelodiscus axenaria*. Males above, females below (none collected); all from Longsheng, Guangxi Zhuang Autonomous Region, China. Not to scale.

Description of the holotype. Carapace length (CL) 100.5 mm, carapace width (CW) 88.1 mm, plastron length (PL) 74.4 mm, head width (HW) 19.8 mm, eye diameter 6.6 mm, interorbital distance 4.1 mm, snout length (SL) 8.9 mm. Carapace oval, slightly domed but with a strong median keel, widest at level of the posterior buttress spurs of the hypoplastra. Marginal ridge low, central tubercle indistinct. Dorsal surface roughened by longitudinal ridging and smaller protuberances spread over the leathery margin. The olive clay-coloured carapace is adorned with an extremely complex greenish black pattern consisting of reticulations and stellate spots, some enclosed by incomplete rings of the same colour, that give it a marbled appearance. Even though the reticulations extend roughly from the outer (pleural) sutures of the neurals laterally and posteriorly to the periphery of the shell, the two halves of the "saddle" are interconnected by several blotches across the vertebral line. Black stellate spots are scattered over the carapace but are well camouflaged in their heavily patterned surroundings. Entoplastron boomerang-shaped, the amount of bending of the transverse bar between the two posteriolaterally directed rami >90°. Callosities are small and present on the ento-, hyo-hypo- and xiphiplastra. Ventral surfaces are yellowish white suffused with cream yellow on the extremities and the leathery margin. Bridge and underside of leathery margin bear some vague bruise-like grey marks that are best defined along the shell borders. Fore- and hindfeet are well-webbed, having five digits each, with claws on the first three digits only. Each forelimb with four antebranchial scales, three of them free-edged. Each hindlimb with two horny scales, one smooth on the posterodorsal surface while the other, which is free-edged, is located on the posteroventral surface. Tail short, barely extending beyond the rear margin of the carapace and indicating the female gender of the specimen. Head extended to posterior level of eyes, terminating in flexible snout. Jaws closed, each covered by fleshy lips except anteriorly where the horny beaks are exposed. Top of head and snout with black splotches on an olive clay-coloured ground. Pre-, sub- and postocular stripes are thick but incomplete, not well discernible among the other markings. The chin is grey brown with pale stipples, the throat dark grey, finely spotted with black; lips are olive clay-coloured with yellow and black dappling.



FIGURE 4. Dorsal and ventral aspects of the holotype of *Pelodiscus shipian* sp. nov. (JNU 20190011, adult female, 100.5 mm CL).

Variation. CL ranges from 74.1 mm to 103.2 mm, PL from 54.6 mm to 76.5 mm in our type series consisting of 28 specimens. Measurements are given in Table 2. Males have a proportionally bulkier head (PL/HW = 3.37-3.99, mean = 3.60 in males, 3.18-4.20, mean = 3.77 in females; HW/SL = 1.80-2.30, mean = 2.00 in males, 1.69-2.44, mean = 1.95 in females) as well as a much longer and thicker tail. Sexual dimorphism is clearly apparent at a PL of 54.6 mm (JNU 20190010) or possibly even earlier. However, it is presently unknown at what size sexual maturity is reached in this species. According to our data, the two genders may attain similar sizes in *Pelodiscus shipian* **sp. nov.**, unlike in *P. axenaria*, in which males seem to grow larger than females (Zhou *et al.* 1991; S. Gong pers. obs.).

TABLE 2. Straight-line measurements (in mm) of the type series of Pelodiscus shipian sp. nov. at Jinan University,
Guangzhou (JNU). CL = carapace length, CW = carapace width, PGW = plane of greatest width of carapace, PL = plas-
tron length $HW =$ head width $SL =$ shout length $OD =$ eve diameter $IOD =$ interorbital distance

Specimen	Sex	CL	CW	PGW	PL	HW	SL	OD	IOD
JNU 20190001	male	100.1	88.5	59.9	72.3	21.2	9.2	7.1	4.1
JNU 20190002	male	98.3	83.7	57.6	72.1	20.1	10.2	6.5	4.1
JNU 20190003	male	92.9	77.9	51.4	66.1	19.2	9.1	6.4	4.1
JNU 20190004	male	81.1	72.0	45.0	60.0	17.8	8.5	6.1	3.4
JNU 20190005	male	84.1	72.1	43.0	62.5	16.9	9.4	6.2	3.8
JNU 20190006	male	91.7	76.1	54.6	66.1	18.2	9.0	5.6	4.0
JNU 20190007	male	81.6	70.8	47.2	61.9	17.4	9.1	6.8	3.1
JNU 20190008	male	82.3	66.6	49.7	67.5	16.9	8.1	5.9	3.2
JNU 20190009	male	83.1	71.4	49.8	62.6	16.6	8.2	5.8	3.1
JNU 20190010	male	74.1	64.9	41.9	54.6	16.5	7.1	6.3	3.0
JNU 20190011 (holotype)	female	100.5	88.1	52.5	74.4	19.8	8.9	6.6	4.1
JNU 20190012	female	88.2	77.6	45.6	67.8	18.1	9.5	5.1	3.7
JNU 20190013	female	88.0	75.8	45.2	64.0	18.6	8.9	6.2	4.2
JNU 20190014	female	90.2	78.2	50.9	66.5	17.0	8.9	6.4	3.8
JNU 20190015	female	88.0	76.8	41.1	65.1	17.6	7.2	5.0	3.9
JNU 20190016	female	89.4	80.6	50.2	58.8	18.5	8.9	5.8	3.8
JNU 20190017	female	82.1	76.7	45.6	62.9	15.6	9.0	5.9	3.5
JNU 20190019	female	86.1	74.2	49.8	61.9	15.9	8.9	5.6	3.7
JNU 20190020	female	96.8	84.4	59.4	74.4	18.9	8.5	5.5	4.0
JNU 20190021	female	86.4	75.5	43.4	64.0	16.0	9.2	5.9	3.1
JNU 20190022	female	86.5	76.9	50.6	64.4	16.4	9.7	6.3	4.1
JNU 20190023	female	85.8	70.1	45.9	65.1	15.5	9.1	5.7	3.1
JNU 20190024	female	78.6	72.6	45.1	63.0	15.1	8.9	6.1	3.2
JNU 20210002	female	88.2	81.6	57.3	69.8	18.9	10.5	5.4	3.1
JNU 20210003	female	84.3	80.3	52.9	68.5	19.5	9.9	4.9	3.5
JNU 20210004	male	103.2	83.1	58.2	76.5	21.3	11.6	5.6	4.4
JNU 20210005	male	88.7	77.4	59.7	67.7	18.9	10.3	5.6	3.5
JNU 20210006	female	80.3	69.5	44.5	61.7	17.1	9.3	5.3	3.1

Pattern intensity varies considerably in *Pelodiscus shipian* **sp. nov.** Whereas the carapace of some individuals, such as the holotype (JNU 20190011; 74.4 mm PL) and one paratype (JNU 20190013; 64 mm PL), both females, has a decidedly marbled appearance, the pattern bears a more striking resemblance to leaf camouflage with more conspicuous stellate spots in others (e.g., paratypes JNU 20190001, 20190007, males; JNU 20190016, 20190017, 20210006, females) or is almost imperceptible due to a general darkening of the ground colour (e.g., JNU 20190002, 20190004, 20190008, 20190010, males; JNU 201900012, 20190019, females); see Figure 6 for examples. The plastron is typically unmarked except for some colour suffusion resembling bruising along its anterior perimeter and

relatively small fuzzy-edged blotches behind the axillae. However, these markings may occasionally extend medially, covering much of the plastral forelobe but never actually contacting the entoplastron (JNU 201900005, male; JNU 201900012, 201900017, both females). The black markings on either side of the tail typical for *P. axenaria* are absent in *P. shipian* **sp. nov.**, but melanistic specimens may display some dark pigmentation on their thighs (e.g., JNU 201900005, male; JNU 201900012, 20210006, both females). Two examples are shown in Figure 6. The lateral bands on the neck are bright yellow in smaller specimens, particularly males (e.g., JNU 201900010), and lose definition with increasing age/size but usually remain discernible in both sexes.



FIGURE 5. One of the paratypes of *Pelodiscus shipian* sp. nov. (JNU 20210002, adult female, 88.2 mm CL) in life.

Distribution. The exact geographical range of *Pelodiscus shipian* **sp. nov.** is unknown at present. Apart from the type locality, the Liaohe River in Fengxin County, Jiangxi, specimens have been obtained in the counties of Shaoyang and Taoyuan and the City of Yongzhou (Hunan Province), suggesting sympatry or confusion with *P. axenaria*.

Originally, the distribution range of *P. axenaria* was believed to encompass the counties and cities of Taoyuan, Pingjiang, Rucheng, Lingling, and Shaoyang in Hunan Province, China (Zhou *et al.* 1991). However, all specimens that we could obtain from Taoyuan and Shaoyang Counties are *P. shipian* (see our paratype series); our neotype of *P. axenaria* comes from Tongdao County in Hunan Province. The records from Zhou *et al.* (1991) were not genetically verified, so that we cannot exclude that some of them referred to *P. shipian*. However, genetically verified records of *P. axenaria* (Chen *et al.* 2005, 2006; Yang *et al.* 2011; Gong *et al.* 2018) are known from Shaoguan (Guangdong), Longsheng and Quanzhou (Guangxi) and from Changde and Anren (Hunan). This suggests that *P. axenaria* and *P. shipian* at least occur in closest proximity, if not in sympatry, in Hunan (Fig. 7).

Another small-bodied *Pelodiscus* species, *P. parviformis*, was described from Guangxi and Hunan (Tang 1997). *Pelodiscus parviformis* is morphologically and genetically distinctive (Gong *et al.* 2018; Farkas *et al.* 2019). Nevertheless, it is possible that some genetically unconfirmed records for *P. parviformis* refer to *P. axenaria* or *P. shipian*.

Our map (Fig. 7) collates for the P. axenaria complex the currently known genetically verified records.



FIGURE 6. Variation in colouration and pattern in *Pelodiscus shipian* **sp. nov.** Freshly dead paratypes JNU 20210005 (male, top and bottom left), JNU 20210004 (male, top right) and JNU 20210006 (female, bottom right), all from Hunan Province, China. Not to scale.

Etymology. The name '*shipian*' is the romanisation of 石片 (shi pian, Chinese for "slab"), derived from the local (Fengxin, Jiangxi) name of the species 石片鳖 (shi pian bie = stone slab soft-shelled turtle) that alludes to its resemblance to a flat stone. The suggested English common name refers to the same feature. The scientific species name is used as a noun in the nominative singular in apposition to the generic name (ICZN 1999: Article 11.9.1.2).



FIGURE 7. Genetically verified records for species of the *Pelodiscus axenaria* complex in central China (compiled from Chen *et al.* 2005, 2006; Yang *et al.* 2011; Gong *et al.* 2018, 2021 and this study). Blue: *P. axenaria*, red: *P. huangshanensis*, green: *P. shipian* **sp. nov.**

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APPENDIX

Specimens examined

Institutional codes follow Sabaj (2020).

Pelodiscus axenaria: CIB 95413–95417, JNU 20210001; identities have been genetically confirmed.

Pelodiscus huangshanensis: ANU 20210001, ANU 20210002, ANU 20210004, ANU 20210005, CIB 116368, SNHM 5414.

Pelodiscus shipian: JNU 20190001-20190017, JNU 20190019-20190024, JNU 20210002-20210006.