

(bp) of the 5'-end of the 16S rRNA gene was selected for amplification by the polymerase chain reaction (PCR) using the primers 1471 (5'-CCTGTTTANCAAAAACAT-3') and 1472 (5'-AGATAGAAACCAACCTGG-3') (Crandall and Fitzpatrick 1996). A portion of the mitochondrial COI gene was amplified by PCR using the primers LCO1490 (5'-GGTCAACAAAT-CATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCA-GGGTGACCAAAAATCA-3') (Folmer *et al.* 1994). The PCR conditions for the above primers were 50s 94°C / 70s 45°C / 60s 72°C (denaturation/annealing/extension), followed by 72°C extension for 10 min.

Sequences were obtained by automated sequencing (ABI PRISM 377 Sequencer and MegaBACE DNA Analysis System 500, Amersham, UK) and were aligned with the aid of CLUSTAL W (version 1.4, Thompson *et al.* 1994) and BIOEDIT (version 5.09, Hall 2001), after verification with the complementary strand. Sequences of the different haplotypes have been deposited in the DDBJ (DNA Data Bank of Japan, accession nos. AB265227 to AB265250).

The best-fitting model for sequence evolution of the combined 16S and COI was determined by MrModeltest (version 2.2, Nylander 2005), selected by AIC (Akaike information criterion), and was subsequently applied for a neighbour-joining (NJ) analysis and a Bayesian inference (BI). The NJ tree was constructed with the program MEGA2 (version 2.1, Kumar *et al.* 2001) using gamma correction obtained from MrModeltest, the Kimura (1980) two-parameter model, 2000 bootstrap reiterations, and complete deletion for the gap. Bayesian analyses were performed with MrBayes (version 3.1.1, Ronquist and Huelsenbeck 2003) using the model selected by MrModeltest. The search was run with four chains for one million generations, with trees being sampled every 100 generations (the first 500 trees were discarded as 'burnin'), replicated four times. The maximum parsimony (MP) tree was constructed by the program PAUP* (version 4.0b10, Swofford 2001) with 2000 bootstrap reiterations, using a simple heuristic search, TBR (tree bisection-reconnection) branch-swapping and 100 random-addition sequence replications. All characters were equally weighted. Gaps in MP tree construction were coded as

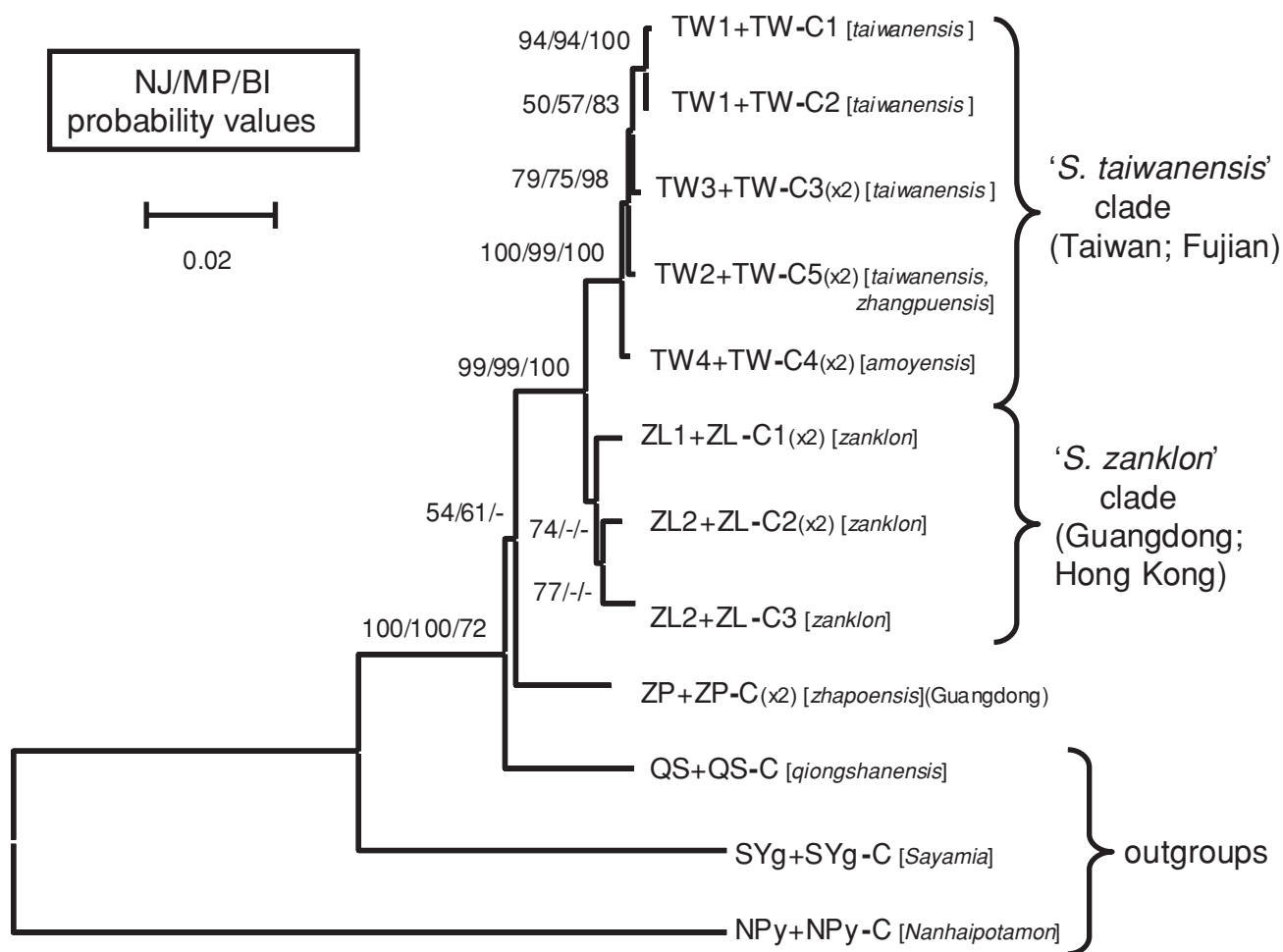


Fig. 2. A neighbour-joining (NJ) tree of the *Somanniathelphusa* species from Taiwan and the Chinese coastal regions based on 1212 base pairs of the combined 16S rRNA and cytochrome oxidase I genes. Probability values at the nodes represent bootstrap values for NJ and maximum parsimony (MP), and posterior probability for Bayesian inference (BI). The species name(s) beside the haplotype was the species identified based on morphological traits. For haplotype abbreviations see Table 1.

missing data. The best-fitting model determined by MrModeltest was then applied to estimate inter- and intra-population genetic diversity using PAUP*.

Results

A 550-bp segment (excluding the primer regions) of the 16S mtDNA gene from 15 specimens was amplified and aligned. Eleven positions were variable and one was parsimony informative. Among the total number of sequences, seven different haplotypes could be distinguished (Table 1). The studied segment of 16S sequences is AT rich (71.2%) (T: 35.2%, A: 36.0%, G: 19.3%, C: 9.5%). For the COI gene, a 658-bp segment from the ingroups was amplified resulting in eight different haplotypes. The studied segment of COI sequences is also AT rich (63.9%) (T: 36.5%, A: 27.4%, G: 16.0%, C: 20.2%). In this gene, 46 positions were variable and 16 were parsimony informative.

The best model calculated by MrModeltest is the GTR+I+G model (Posada and Crandall 1998) for combined 16S and COI with 1212 bp (gamma distribution shape parameter = 0.8927). The phylogenetic tree constructed from NJ analysis, with the bootstrap values from MP and BI analyses, is shown in Fig. 2. Only bootstrap values larger than 50% are shown.

Two major groups could be separated based on the combined 16S and COI tree (Fig. 2). One major group comprises just *S. zhapoensis*. The second group, containing the remaining species, has two smaller clades, one including the specimens from Fujian and Taiwan (supported by all three methods) and a second clade distributed in Eastern Guangdong (and Hong Kong) (supported by the NJ method). Considering the known geographical distributions of these two clades, the first is here referred to as the '*S. taiwanensis*' clade, and the second, the '*S. zanklon*' clade (see Discussion for details).

Among the haplotypes of the '*S. taiwanensis*' and '*S. zanklon*' clades, the difference of nucleotide number is within 3 bp (average 2.0) and 1 bp for 16S, and 6 bp (average 4.3) and 11 bp (average 9.3) for COI respectively; the divergence is within 0.40% (average 0.20%) and 0.20% for 16S, and 0.89% (average 0.63%) and 1.64% (average 1.39%) for COI respectively (Tables 2, 3). The average difference in nucleotide

numbers between the '*S. taiwanensis*' and '*S. zanklon*' clades is 2.5 bp (1–4) for 16S and 15.3 bp (13–20) for COI, and the average divergence is 0.40% (0.20–0.61%) for 16S and 2.39% (2.01–3.18%) for COI.

Discussion

During the glacial periods, Guangdong, Fujian and Taiwan were all connected by a land bridge (see Boggs *et al.* 1979; Voris 2000). Based on the postulated paleo-drainage system of the Taiwan continental shelf during the most recent glacial period *c.* 15000 years ago (when the sea level was 140 m below the present level) (Boggs *et al.* 1979), the ancestral Minjiang River from Fujian was connected to the Jhuoshuei River from west-central Taiwan, with both flowing into the ancestral estuary south of the area between Penghu and Taiwan (Fig. 3). Using this land bridge, many terrestrial animals (e.g. elephants, rhinoceros, carnivores, etc.) are believed to have migrated from China to Taiwan during this glacial period, as shown by the numerous fossils found from the Taiwan Strait and western Taiwan (You *et al.* 1995; Ho *et al.* 1997, 2000; Cai 1999). The Lianhua Range, located in the eastern part of Guangdong Province, near Fujian Province, with altitudes of 1336–1559 m above sea level, extends almost all the way to the seashore (Shanwei, Guangdong Province; Fig. 1) and may have acted as an isolating barrier for flightless and less mobile animals.

The monophyly of the '*S. taiwanensis*', and '*S. zanklon*' clades corresponds with their distribution, with their members occupying the plains from the Zhujiang estuary east to Fujian and Taiwan. Group members would have easily dispersed during the glacial periods. However, the Lianhua Range would have probably played a key part in geographically isolating representatives of the '*S. taiwanensis*' and '*S. zanklon*' clades during interglacial periods. As the last glacial event was relatively recent (*c.* 15000 years ago) (see Voris 2000), the two clades would only have been effectively isolated for a relatively short time. Since the populations of *S. taiwanensis* are restricted to west-central Taiwan and have failed to spread further, dispersal from China is hypothesised to be a recent event. It is likely that the ancestors of *S. taiwanensis* migrated from Fujian through the Paleo-Minjiang River to the Jhuoshuei River. As argued, the

Table 2. Pairwise nucleotide percentage divergence matrix (lower-left) and the basepair differences (upper right) based on 550 basepairs of the 16S rRNA gene between the haplotypes of *Somanniathelphusa* (Table 1) collected from Taiwan, Hong Kong, Hainan Island and the Chinese coastal provinces (Guangdong and Fujian)

Nucleotide divergence is estimated from pairwise distance of nucleotides based on the calculated GTR+I+G model of nucleotide substitution. For abbreviations of haplotypes see Table 1. Types of basepair differences are abbreviated as follows: s for transitions, v for transversions, and i for indels.

	' <i>S. taiwanensis</i> ' clade				' <i>S. zanklon</i> ' clade		<i>S. zhapoensis</i>	<i>S. qiongshanensis</i>
	TW1	TW2	TW3	TW4	ZL2	ZL2	ZP	QS
TW1	—	1s,1i	2s,1i	1s,2i	3s,1i	2s,1i	6s,2v,1i	9s,2v,2i
TW2	0.20	—	1s	1i	2s	1s	5s,2v	8s,2v,1i
TW3	0.40	0.20	—	1s,1i	3s	2s	6s,2v	9s,2v,1i
TW4	0.20	0.00	0.20	—	2s,1i	1s,1i	5s,2v,1i	8s,2v,2i
ZL1	0.60	0.40	0.61	0.40	—	1s	7s,2v	8s,2v,1i
ZL2	0.40	0.20	0.40	0.20	0.20	—	6s,2v	7s,2v,1i
ZP	1.74	1.51	1.75	1.51	1.98	1.75	—	7s,2v,1i
QS	2.43	2.20	2.45	2.20	2.18	1.96	1.97	—

very high similarity in genotypes between *S. taiwanensis* and its sister taxa from Fujian (Fig. 2, Tables 2, 3), as well as the restricted distribution of *S. taiwanensis* (only in west-central Taiwan) (Fig. 3), suggests that this occurred very recently, perhaps as recently as the last glacial event.

The 16S and COI haplotype differences between Taiwan and Fujian (0–3 bp and 3–6 bp, respectively) (Table 2), suggest a transoceanic dispersal of representatives of the ‘*S. taiwanensis*’ clade from Fujian to Taiwan may still have been possible owing to the relatively high salinity tolerance of *Somanniathelphusa* proposed by Dai (1999). Members of this genus inhabit lowland coastal plains, even close to the seashore (Ng and Dudgeon 1992; Dai 1999), and Dai (1999) considered it as a kind of ‘marine group’ of freshwater crabs. However, the degree of salinity tolerance and the dispersal pathway of *S. taiwanensis* are still unknown and future studies are necessary to ascertain these. Interestingly, transoceanic dispersal has also been suggested to explain the divergence of freshwater crabs between the continental Africa and Madagascar (Daniels *et al.* 2006).

Three species of the genus *Somanniathelphusa* are currently known from Fujian, *viz.* *S. amoyensis*, *S. zhangpuensis*, and *S. huaanensis* Naiyanetr & Dai, 1997 (Naiyanetr and Dai 1997; Dai 1999). Four species of *Somanniathelphusa* are known from Guangdong and Hong Kong (Ng and Dudgeon 1992; Dai 1999), *viz.* *S. sinensis* (H. Milne Edwards, 1853), *S. zanklon*, *S. yangshanensis* Naiyanetr & Dai, 1997, and *S. zhapoensis*. The identity of the true *S. sinensis*, ostensibly the most common lowland species of *Somanniathelphusa* in China (Bott 1970; Dai 1999) is a major problem. Ng and Dudgeon (1992) recharacterised and refigured the species after examining the lectotype and paralectotypes of *S. sinensis* and argued that many of the old records of the species must be rechecked. Dai (1999), however, in her synopsis of the Chinese freshwater crab fauna, inexplicably did not consider Ng and Dudgeon’s (1992) reappraisal of the species and merely followed old records for what she regarded as ‘*S. sinensis*’ (see Ng 2000), using only specimens from and near Guangzhou, Guangdong Province. Certainly, on the basis of her figures of the species (Dai 1999: 68, Fig. 29), her material is not *S. sinensis s. str.*, and is more likely to be *S. zanklon*, or another allied taxon. Hong Kong is immediately south of Guangzhou

and is in the same geographic zone. The only way objectively to resolve this taxonomically is for all Dai’s (1999) material to be re-examined and critically compared with the types of *S. sinensis* and *S. zanklon*. Comparison of the figures of the various species in the papers of Ng and Dudgeon (1992), Naiyanetr and Dai (1997) and Dai (1999), suggests that the real *S. sinensis* appears to be morphologically closest to the three new species described by Naiyanetr and Dai (1997): *S. amoyensis* (Fujian Province), *S. yuilinensis* (Jiangxi Province) and possibly *S. araeochela* (Jiangxi Province).

As noted by Ng and Dudgeon (1992), the collector of the types of *S. sinensis* was M. Callery, who obtained numerous natural history specimens from East China in the 1800s. Callery’s collections are mainly from the east coast of China, and Macao, but also from near Chusan (= Zhoushan, Zhejiang Province), Shanghai, Ning-Po (= Ningbo, Zhejiang Province) and Amoy (= Xiamen, Fujian Province). He also had material from Batavia and the Philippines. All of Callery’s material of *S. sinensis* was labelled as being from China without specific details. On the basis of this historical data, the taxonomic interpretation of the species and what is presently known about *Somanniathelphusa*, the real *S. sinensis* is likely to be closest to, if not identical with, *S. amoyensis*. While it is also likely that Callery had material from Macao, no fresh material of any primary or secondary freshwater crab has been collected there for many years, as the freshwater systems there have suffered substantially from anthropogenic changes (see Chan *et al.* 2005). Certainly we know of no *Somanniathelphusa* material, recent or otherwise from Macao. On the basis of these data, we prefer to exclude further reference to *S. sinensis s. str.*, or discuss its status, at least until the necessary taxonomic comparisons have been done.

Of the three species of *Somanniathelphusa* known from Fujian, we collected *S. amoyensis* and *S. zhangpuensis* from their respective type localities, Xiamen and Zhangpu. We did not manage to obtain *S. huaanensis* from its type locality, Hua-an. All three type localities are within a 100 km radius in a completely flat coastal area. For Guangdong and Hong Kong, we obtained *S. zhapoensis* from the western coastal area of Guangdong, and *S. zanklon* from the eastern part (including

Table 3. Pairwise nucleotide percentage divergence matrix (lower-left) and basepair differences (upper-right) based on 658 basepairs of the cytochrome oxidase I gene between the haplotypes of *Somanniathelphusa* (Table 1) collected from Taiwan, Hong Kong, Hainan Island and the Chinese coastal provinces (Guangdong and Fujian)

Nucleotide divergence is estimated from pairwise distance of nucleotides based on the calculated GTR+I+G model of nucleotide substitution. For abbreviations of haplotypes see Table 1. Types of basepair differences are abbreviated as follows: s for transitions and v for transversions.

	‘ <i>S. taiwanensis</i> ’ clade				‘ <i>S. zanklon</i> ’ clade			<i>S. zhapoensis</i>	<i>S. qiongshanensis</i>
	TW-C1	TW-C3	TW-C4	TW-C5	ZL-C1	ZL-C2	ZL-C3	ZP-C	QS-C
TW-C1	—	3s	5s,1v	5s	14s,2v	19s,1v	16s,1v	26s,7v	34s,7v
TW-C3	0.43	—	4s,1v	2s	11s,2v	16s,1v	13s,1v	26s,7v	31s,7v
TW-C4	0.89	0.73	—	4s,1v	10s,3v	14s,2v	11s,2v	24s,8v	29s,8v
TW-C5	0.73	0.29	0.74	—	11s,2v	16s,1v	13s,1v	26s,7v	31s,7v
ZL-C1	2.52	2.01	2.02	2.02	—	10s,1v	7s,1v	23s,5v	27s,5v
ZL-C2	3.18	2.66	2.51	2.67	1.64	—	9s	23s,6v	28s,6v
ZL-C3	2.68	2.17	2.02	2.18	1.19	1.33	—	24s,6v	29s,6v
ZP-C	6.21	6.15	5.85	6.19	4.84	5.07	5.30	—	27s,4v
QS-C	7.78	7.11	6.90	7.16	5.65	6.06	6.30	5.41	—

Hong Kong). We did not manage to obtain material of *S. yangshanensis* from the northern montane area of Guangdong (its type locality).

The difference in the sequences of the 16S rRNA among *S. amoyensis*, *S. taiwanensis*, *S. zanklon* and *S. zhangpuensis* from eastern Guangdong, Fujian, and west-central Taiwan, is within four base pairs. Based on the molecular studies of species of *Geothelphusa* from southern Taiwan (Shih *et al.* 2004) and *Nanhaipotamon* from Taiwan and Fujian (Shih *et al.* 2005), these species of the genus *Somanniathelphusa* are either sibling taxa or perhaps even synonyms. However, the specimens from Taiwan and Fujian form a clade supported by the combined 16S and COI data (all three methods), in contrast with another clade distributed in eastern Guangdong and Hong Kong (NJ method) (Fig. 2). As has been discussed, the western Guangdong *S. zhapoensis* falls into its own clade and there is an average difference of 8.2 bp in the 16S between *S. zhapoensis* and the other species (Table 2).

It seems clear that *S. zhapoensis* is a distinct species, forming a group separate from the others. The other species studied here

are much more closely related. Different interpretations are possible. It is possible that *S. amoyensis*, *S. taiwanensis*, *S. zanklon*, and *S. zhangpuensis* are all one species. This is difficult to reconcile with their morphological taxonomic characters, with *S. zanklon* possessing a different carapace form and gonopod from *S. amoyensis*. *Somanniathelphusa taiwanensis* itself has a relatively stouter gonopod. A second possibility is that we have two subspecies here, one, *S. zanklon*, and other encompassing *S. taiwanensis*, *S. amoyensis* and *S. zhangpuensis*. This is also awkward as the morphological traits of *S. taiwanensis* are quite different from the other two sister taxa. However, as discussed earlier, until the changes associated with growth are properly studied, the quantum of intraspecific variation understood, and clinal variations better documented, any action to synonymise these taxa must be regarded as premature. The molecular data, however, leaves little doubt as to their close relationship.

In Taiwan, the distribution of *S. taiwanensis* itself is relatively patchy within the west-central part, *viz.* Nantou County (Jhushan: Chiu 1964); Yunlin County (Shihguei: Chiu 1964; this study; Gukeng and Douliou: Shy *et al.* 1996; Linnei: Ho 1998);

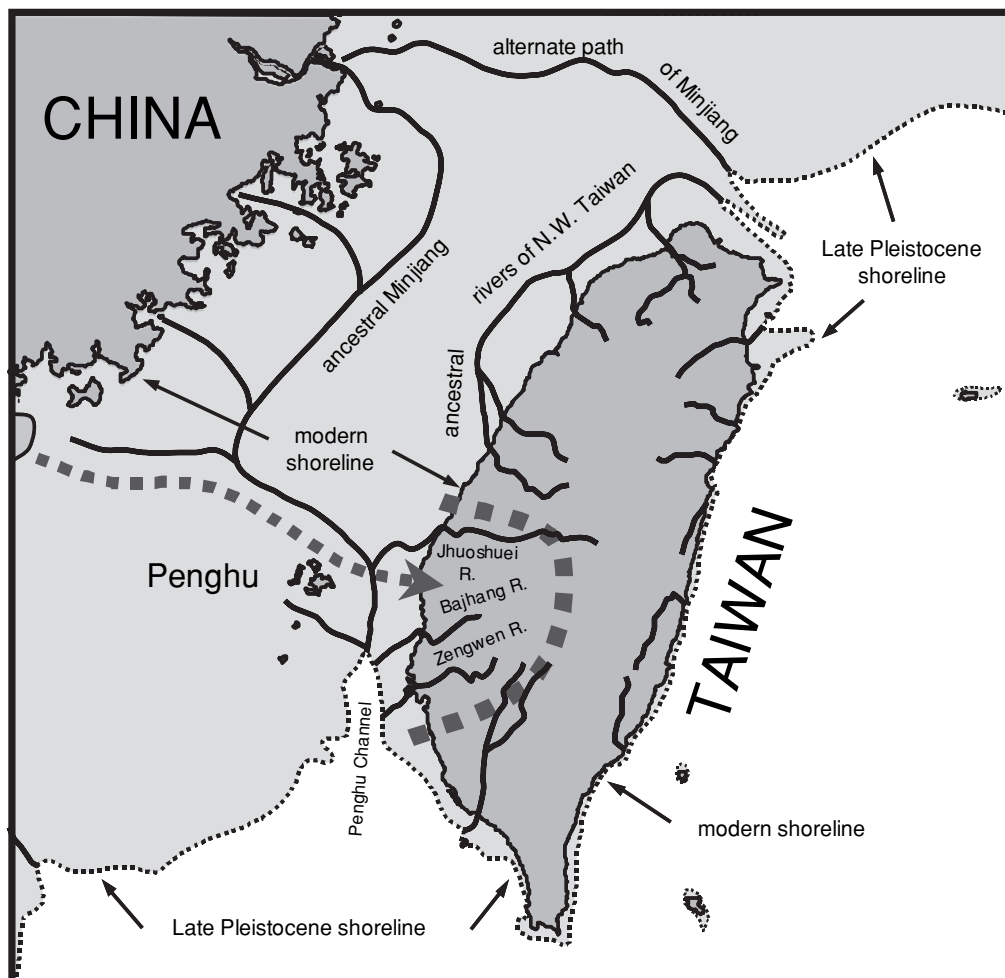


Fig. 3. A postulated paleo-drainage system on the Taiwan continental shelf during glaciations in Late Pleistocene (~15000 years ago). Sea level is assumed to be 140 m below the present level (modified from Boggs *et al.* 1979). The broken line in west-central Taiwan indicates the present distribution of *Somanniathelphusa taiwanensis*. The arrow from China to Taiwan indicates the possible dispersal pathway of the '*S. taiwanensis*' clade during glaciations.

Chiayi County (Bott 1968, 1970; Hwang and Mizue 1985; Meishan: Chiu 1964; Minei 1974; Shueishan: Shy *et al.* 1996); Tainan County (Guanzhilin: Terao 1915; Wushulin, Baihe: this study; Lioujia: Maki and Tsuchiya 1923; Madou: Chiu 1964). The records from northern (Shenkeng, Taipei County: Terao 1915) and eastern Taiwan (Taitung: Sakai 1939) cannot be confirmed but are doubtful in view of what is now known, and no specimens exist or have been found from these areas. It is interesting to comment that there are two records of parathelphusids from Japan. *Sayamia germaini* (Rathbun, 1902) (as *Potamon (Parathelphusa) germaini*) was reported to occur in Japan (Rathbun 1905) and *Oziotelphusa bouvieri* (Rathbun, 1904) (as *Parathelphusa (Oziotelphusa) bouvieri*) was recorded from Nagasaki, Kyushu, Japan (Balss 1914). These records were questioned by Sakai (1976), and we agree that they are clearly incorrect. *Sayamia germaini* is known only from Thailand (Naiyanetr 1994) whereas *Oziotelphusa bouvieri* is endemic to India (Bahir and Yeo 2005). Thus, the only true record of native parathelphusids in any East Asian island is from the west-central part of Taiwan, that is, *S. taiwanensis*.

Although members of the '*S. taiwanensis*' clade are distributed from Taiwan, Fujian Province, to the eastern part of Guangdong Province, the populations of the various taxa in Taiwan and Fujian are relatively small. Their habitats in the plains have been severely damaged by development and the remaining populations are restricted to irrigation ditches near the paddy fields. The extensive use of insecticides and herbicides on the rice-paddies is an immediate danger to their continued survival.

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