

A COMPARISON OF THE MICROMORPHOLOGY OF THE G1 OF  
FRESHWATER CRABS OF THE GENUS *GEOTHELPHUSA* (BRACHYURA,  
POTAMIDAE) FROM TAIWAN

BY

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ABSTRACT

Scanning electron microscopy (SEM) was used to compare the micromorphology of the male first gonopods (G1) of 22 species of common Taiwanese potamid crabs of the genus *Geothelphusa* Stimpson, 1858. Electron micrographs were taken from dorsal, lateral, and apical views of the terminal segment, the sub-terminal segment, and the synovial membrane; and a total of five measurements was taken, i.e., synovial membrane length (SML) and width (SMW), sub-terminal segment width (SW), and terminal segment length (TSL) and width (TSW). In addition, the diameter of the apical opening of the ejaculatory canal (AD), the number of scale rings, the setal type, and the direction of the curve of the tip of the terminal segment were recorded. In adult female crabs, the mean of the diameter of the gonopores and the distance between these were also measured. The scanning electron micrographs of the G1 are all shown in the present paper.

RÉSUMÉ

La microscopie électronique à balayage (SEM) a été utilisée pour comparer la micromorphologie des premiers gonopodes mâles (G1) de 22 espèces communes de crabes Potamidae de Taiwan du genre *Geothelphusa* Stimpson, 1858. Les microphotographies du segment terminal, du segment sub-terminal et de la membrane synoviale ont été prises en vues dorsales, latérales et apicales; un total de cinq mesures a été effectué, soient la longueur de la membrane synoviale (SML) et sa largeur (SMW), la largeur du segment sub-terminal (SW), ainsi que la longueur du segment terminal (TSL) et sa largeur (TSW). De plus, le diamètre de l'ouverture apicale du canal éjaculateur (AD), le nombre des anneaux d'écailles, le type de soies et la direction de la courbe de l'extrémité du segment terminal ont été examinés. Chez les crabes adultes femelles, la moyenne du diamètre des gonopores et la distance entre ces derniers ont été également mesurées. Les microphotographies à balayage des G1 sont toutes présentées dans le présent article.

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## INTRODUCTION

The freshwater crabs of Taiwan comprise two families and four genera, viz., of the Potamidae Ortmann, 1896: *Geothelphusa* Stimpson, 1858, *Nanhaipotamon* Bott, 1968, and *Candidiopotamon* Bott, 1967; and of the Parathelphusidae Alcock, 1910: *Somanniathelphusa* Bott, 1968 (cf. Shy et al., 1994, 2000; Chen et al., 1998, 2003, 2005; Tan & Liu, 1998; Dai, 1999; Shy & Yu, 1999; Ng et al., 2001; Shy, 2005). All four genera include species from China, Japan, or other countries. However, the freshwater crabs from Taiwan belonging to these four genera are all endemic in Taiwan (Shy et al., 1994; Shy & Yu, 1999; Ng et al., 2001). There are 35 species in the genus *Geothelphusa* recorded from Taiwan now. Shih et al. (2004) used the small subsegment of the mitochondrial 16S rRNA encoding gene in partial sequencing (550 bp) to assess the systematics of the southern Taiwanese *Geothelphusa* species. They suggested some species would be synonyms. In view of the biological species concept, variation in the morphology of the copulatory organs should result in rapid reproductive isolation, and hence in acceleration of the speciation process (Mayr & Ashlock, 1991; Schluter, 1996). Therefore, we still use the taxonomic system of Shy et al. (1994) and Ng et al. (2001), which are based on differences in characters of the male first gonopod (G1) to distinguish between species of these freshwater crabs (Ng, 1988; Ng & Naiyanetr, 1993; Shy et al., 1994; Dai, 1999).

The aims of the this study are (1) to investigate the detailed micromorphology of the G1 with scanning electron microscopy (SEM) in order to supplement the gross morphology now depicted in line drawings in the early days of the systematic studies on this genus; (2) to identify species-defining gonopod characters, and thus use the morphology of the G1 as a key character in the taxonomy of the potamids of the genus *Geothelphusa* in Taiwan.

## MATERIAL AND METHODS

For the present study, 22 of the more common Taiwanese species of *Geothelphusa* were selected, and of these topotype specimens were collected from the type locality (Shy et al., 1994). Specimens were examined, preserved in 70% ethanol, and deposited in the Department of Biological Sciences, National Sun Yat-sen University (NSYSU), Kaohsiung, and the National Taiwan Ocean University (NTOU), Keelung. The methods used in scanning electron microscopy by Felgenhauer (1987) were modified to observe the male G1 with the aid of a HITACHI S-2400 SEM equipped with a digital camera that stores the pictures. The pictures thus obtained were next transferred to a computer for comparison. A total of 1-3 individuals of each species was examined by SEM for the right G1,

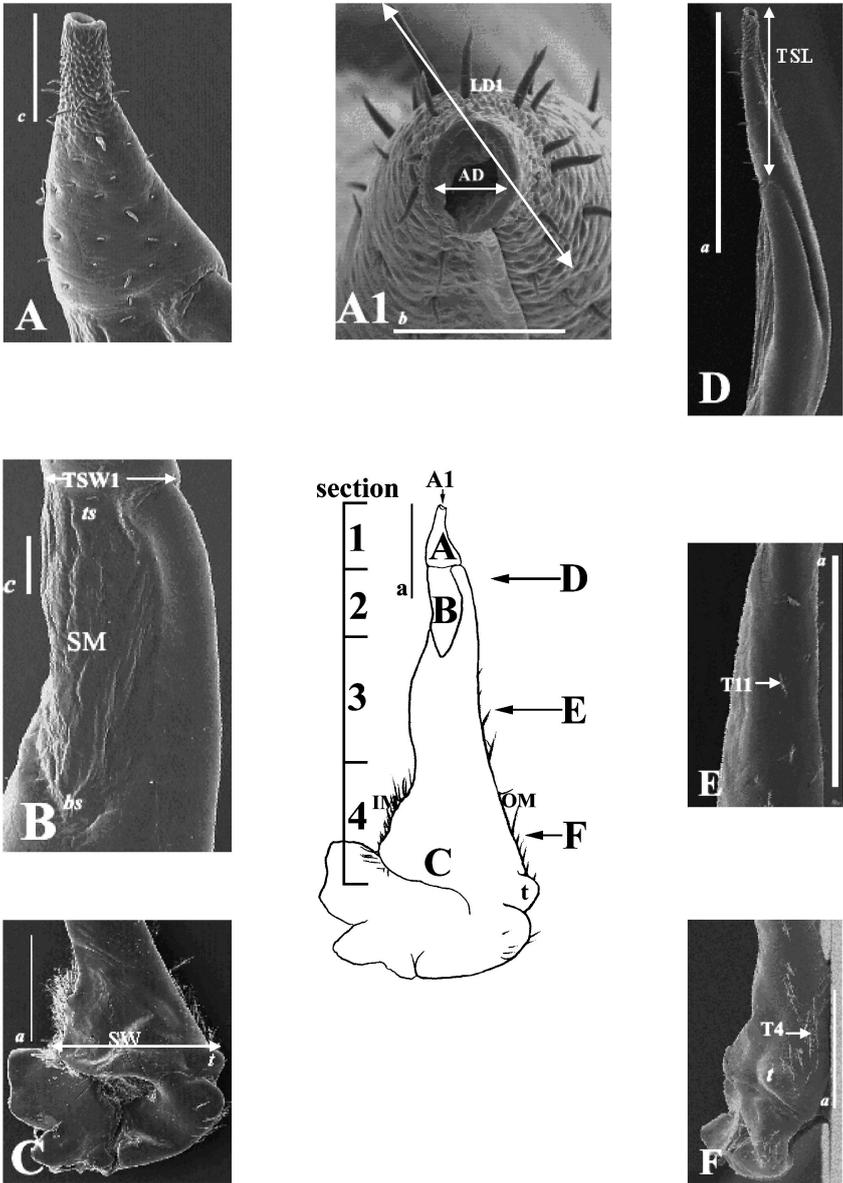


Fig. 1. Micromorphology of the right first gonopod (G1) of *Geothelphusa eucrinodonta* Shy, Ng & Yu, 1994, 15.3 × 11.9 mm (NSYSU F710041), by SEM; middle panel, external morphology (dorsal view) with line drawings. Section 1, terminal segment (A); 2-4, sub-terminal segment (B-C); D-F, lateral view; A1, apical tube aperture of G1 (top view); AD, apical aperture diameter of tube; IM, inner margin; OM, outer margin; SM, synovial membrane; SW, sub-terminal segment width; TSW, terminal segment width; TSL, terminal segment length; *bs*, basal margin of synovial membrane; *ts*, top margin of synovial membrane; *t*, outer proximal margin tooth or protuberance of sub-terminal segment. Some parts are magnified in fig. 2. Scales: *a* = 1 mm; *b* = 100 μm; *c* = 200 μm.

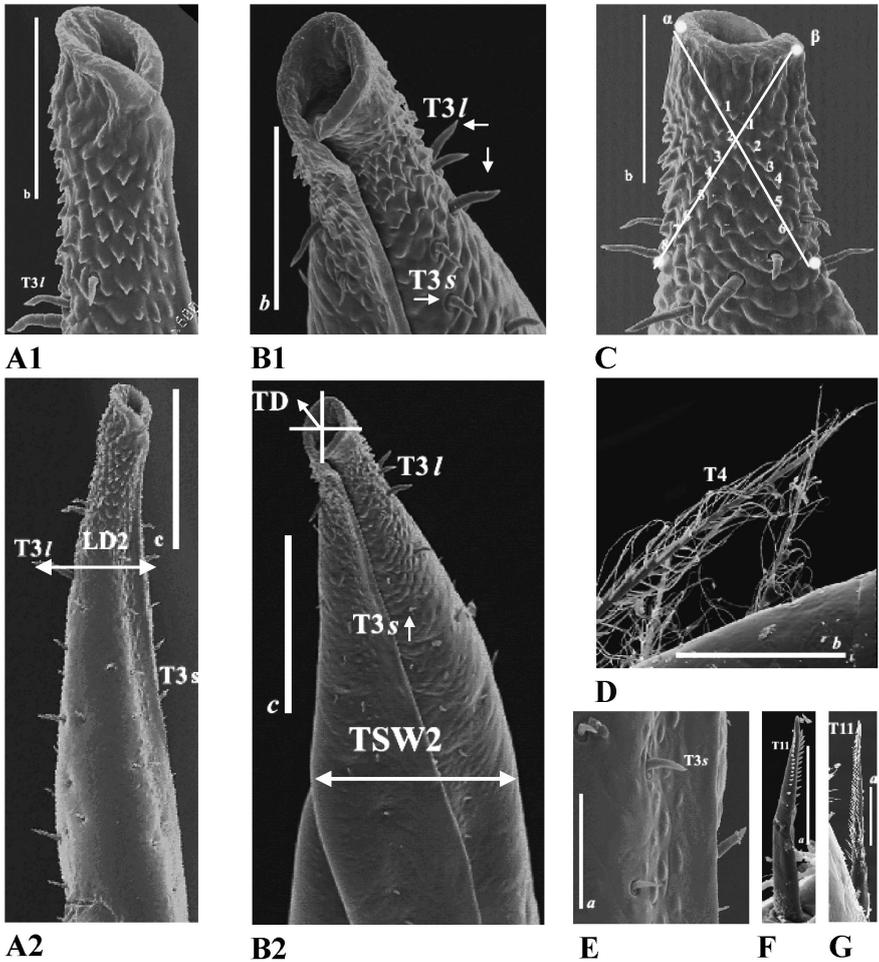


Fig. 2. Micromorphology of the right first gonopod (G1) of *Geothelphusa eucrinodonta* Shy, Ng & Yu, 1994, 15.3 × 11.9 mm (NSYSU F710041), by SEM. A1-2, lateral view; B1-2, ventral view; C, Arabic numerals represent scale rings counted by intersecting diagonals in two directions ( $\alpha$ ,  $\beta$ ); LD, maximum diameter of terminal segments distal part, measured over the longest spines; TD, tip curve direction of G1; TSW, terminal segment width. Setal types: T3, simple; T4, plumose; T11, serrate; *l*, long simple setae, *s*, short simple setae. Scales: *a* = 50  $\mu$ m; *b* = 100  $\mu$ m; *c* = 200  $\mu$ m.

and at least another 2-3 individuals were dissected and checked with an Olympus ZSH10 dissecting microscope, also equipped with a digital camera (Moticam 480, Motic Images Plus 2.0). The scanning electron micrographs of the G1 of some species have already been published in Chen et al. (2003). At present, the 22 common species now treated revealed more details, that could represent elements of a common type of morphology of the G1 of all Taiwanese species of *Geothelphusa*.

The terminology used in this study mostly follows that used by Abele (1971), Ng (1988), Ingle (1992), Shy (1994), and Shy et al. (1994). The measurements and abbreviations taken are shown in figs. 1-2: CW  $\times$  CL, carapace width  $\times$  carapace length; G1, male first gonopods (pleopods); TLG1, total length of G1 in lateral view. The G1 was subdivided into four sections for simplicity of descriptions, i.e., section 1, terminal segment (fig. 1A); 2-4, sub-terminal segment, with section 2, the synovial membrane (SM) (fig. 1B) : SML, length of synovial membrane; SMW, width of synovial membrane; SW, width of sub-terminal segment (fig. 1C). TSW, maximal width of terminal segment from two points of view (TSW1 and TSW2) (figs. 1B, 2B2); TSL, length of terminal segment (fig. 1D); AD, apical aperture diameter of tubes, or diameter of apical opening of ejaculatory canal (fig. 1A1). In addition, we counted the rings of scales on the terminal segment of G1 in two diagonal directions ( $\alpha$ ,  $\beta$ ), i.e., Arabic numerals represent the sequence of rings with scales counted with intersected lines in diagonal directions (fig. 2C); setal types: T3, simple seta, T4, plumose seta, T11, serrate seta (fig. 2D-G); LD, mean maximum diameter of the distal part of the terminal segment, measured from the distance between the opposite sides of the longest spines (LD1 and LD2) (fig. 1A1, 2A2). For the description of the dorsal aspect of the terminal segment in a formula: setal scattered (SS) = ( $l/s$ ),  $l$ : number of long T3,  $s$ : number of short T3 (fig. 2B1, 2); rings of scales (SR) = ( $\alpha - \beta$ ). Tip of G1 (TD) seen in ventral view of terminal segment, curved in direction with angle greater than  $95^\circ$ , curved outwards; smaller than  $85^\circ$ , inwards; and  $86^\circ$ - $94^\circ$ , curved upwards (fig. 2B2). Mean diameter of the female gonopores and distance between the gonopores were also measured.

For comparing the differences in the G1 between species, the ratios (table I) used mainly follow Shy et al. (1994), and include total length of G1 divided by the carapace length of an adult male (TLG1/CL), by the sub-terminal segment width (TLG1/SW), and by the terminal segment length (TLG1/TSL); the apical opening of the diameter of the ejaculatory canal and the largest diameter of the distal part of the terminal segment divided by the largest width of that segment, (AD/TSW) and (LD/TSW), respectively; and the length of the synovial membrane divided by that membrane's width (SML/SMW). The mean gonopore diameter (= (gonopore length + gonopore width)/2) divided by the carapace width of the adult female (GD/CW) was also calculated. Three body-size groups of adult male *Geothelphusa* were recognized: CW > 30 mm, large (group L); 22-30 mm, medium (group M); and <22 mm, small (group S), all after Shy (1994).

TABLE I

A comparative survey of the micro-structures of the first gonopod (G1) in dorsal aspect observed with the SEM on topotypes of freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 from Taiwan; character ratios and abbreviations of terms are described in the text

Species	Character										
	Body size <sup>a</sup>	TLG1 / CL	TLG1 / SW	TLG1 / TSL	AD/ TSW	LD/ TSW	SML/ SMW	SR	SS	Altitude of habitat (m)	GD/CW <sup>b</sup> (×100)
<i>G. albogilva</i>	L	0.33	3.3	6.5	0.20	0.46	4.2	7-11	4/26	100	5.79
<i>G. ancylophallus</i>	L	0.30	2.4	3.5	0.14	0.56	2.9	10-11	4/41	150	5.72
<i>G. bicolor</i>	M	0.34	2.1	5.2	0.16	0.49	3.5	10-11	12/34	100-600	7.98
<i>G. caesia</i>	L	0.35	3.5	5.3	0.17	0.45	3.8	5-7	3/31	100-500	7.36
<i>G. cinerea</i>	M	0.30	3.1	4.9	0.16	0.46	2.8	8-10	5/31	100-600	8.31
<i>G. dolichopodes</i>	M	0.33	5.6	8.1	0.15	0.65	2.9	9-10	9/26	500	7.50
<i>G. eurinodonta</i>	S	0.35	2.5	5.9	0.12	0.40	3.0	6-8	11/18	50	8.44
<i>G. eurysona</i>	S	0.27	5.3	5.3	0.10	0.72	2.3	4-5	7/21	1000	7.29
<i>G. gracilipes</i>	S	0.28	3.2	5.3	0.16	0.85	3.7	7-8	9/28	500-1000	7.45
<i>G. ilan</i>	M	0.29	2.3	6.0	0.17	0.59	3.2	6-7	10/36	300-600	8.65
<i>G. lanyu</i>	S	0.34	2.8	5.5	0.13	0.46	3.0	5-6	2/23	50	9.70
<i>G. lutao</i>	S	0.32	2.4	5.0	0.15	0.49	2.7	5-7	4/34	50	7.65
<i>G. monticola</i>	S	0.33	2.2	4.7	0.17	0.60	2.8	4-5	4/19	1500-2000	8.48
<i>G. nanao</i>	M	0.33	2.8	8.4	0.18	0.53	3.5	8-9	3/27	700	7.92
<i>G. nanhsi</i>	M	0.36	3.2	6.6	0.14	0.37	4.4	14-15	5/27	100-200	8.89
<i>G. olea</i>	L	0.30	2.3	5.1	0.12	0.48	2.8	10-11	3/29	150-1000	7.62
<i>G. takuan</i>	S	0.36	2.4	5.8	0.13	0.65	2.9	6-7	13/20	1500	7.28
<i>G. tali</i>	S	0.31	3.1	4.9	0.15	0.53	3.9	5-6	3/30	100-300	9.74
<i>G. taroko</i>	M	0.31	2.7	6.5	0.28	0.77	4.3	6-8	6/17	850	8.61
<i>G. tawu</i>	S	0.34	3.3	5.3	0.13	0.43	2.7	5-6	5/23	100	7.94
<i>G. tsayae</i>	M	0.32	3.0	6.8	0.11	0.35	3.7	10-11	3/19	100-1000	7.09
<i>G. wutai</i>	M	0.40	4.2	8.3	0.11	0.39	4.0	11-11	2/22	500	7.18

<sup>a</sup> Adult male crabs have been divided into three body-size groups according to carapace width (CW) > 30 mm = large (L); 22-30 mm = medium (M); <22 mm = small (S); after Shy (1994).

<sup>b</sup> Female character: mean gonopore diameter (GD) = (gonopore length + gonopore width)/2, relative to carapace width.

## RESULTS

### Main micromorphological characteristics of the male G1 under SEM

#### Genus *Geothelphusa* Stimpson, 1858

In this genus, the main micromorphological characteristics of the male G1 using SEM were found to be as follows. The total length of G1 (TLG1) is about one-third of the carapace length of an adult male. The terminal segment was slender, and equipped with T3 setae, the numbers of short T3 being higher than those of long

T3 setae, and the distal part equipped with 4-18 rings of scales. The sub-terminal segment is broadened, with a near by quadrangular synovial membrane and a tooth (protuberance) on the proximal outer margin. The proximal margin and the base of the sub-terminal segment have T3, T4, and T11 setae, and on the inner margin the T4 setae are more densely distributed than on the outer margin (fig. 1C-F).

***Geothelphusa albogilva* Shy, Ng & Yu, 1994**

(fig. 3A1-3)

Material examined with SEM. — Male (29.3 × 23.8 mm) (NSYSU F90121502): TLG1 = 7.8 mm; AD = 83 μm; LD = 196.1 μm; SR = 7-11; SS = 4/26; TD = 116°; Bauli, Hengchun, Pingtung county, coll. W.-J. Chen, 15 Dec. 2001.

Other material. — Two males, 2 juveniles (largest male 40.6 × 31.9 mm) (NSYSU F90121507), Bauli, Hengchun, Pingtung county, coll. W.-J. Chen, 15 Dec. 2001; 2 males (largest 38.8 × 32.3 mm) (NSYSU F90071201), Hengchun, Pingtung county, coll. W.-J. Chen, 12 July 2001; 1 male, 1 female (male 33.7 × 26.8 mm) (NSYSU F89111401), Tajen, Taitung county, coll. W.-J. Chen, 14 Nov. 2000; 1 female, 1 juvenile (female 36.0 × 26.4 mm) (NSYSU F90120801), Mutan, Pingtung county, coll. W.-J. Chen, 8 Dec. 2001.

Terminal segment. — Curved outwards and reaching beyond sternal condyle in situ, distal part with 7-11 rings of scales (fig. 3A1) and a maximum diameter of 196.1 μm; dorsal aspect of terminal segment with 4 long T3 setae and 26 short T3 setae (fig. 3A2); diameter of apical opening of ejaculatory canal about 83.0 μm; length and width of base about 1.2 mm and 422.7 μm, respectively.

Sub-terminal segment. — Mean width about 2.4 mm; with synovial membrane of which ratio length : width is about 4.2, basal margin low, concave and top margin rather convex (fig. 3A3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered mainly on section 4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter 2.6-2.8 × 1.8-1.9 mm, distance between pores approx. 2.2 mm.

***Geothelphusa ancylophallus* Shy, Ng & Yu, 1994**

(fig. 3B1-3)

Material examined with SEM. — Male (33.5 × 26.3 mm) (NSYSU F89110401): TLG1 = 8.0 mm; AD = 75.6 μm; LD = 298.7 μm; SR = 10-11; SS = 4/41; TD = 107°; Neimen, Kaohsiung county, coll. W.-J. Chen, 4 Nov. 2000; 1 male (35.5 × 28.7 mm) (NSYSU F90112404), Neimen, Kaohsiung county, coll. W.-J. Chen, 24 Nov. 2001.

Other material. — One male (33.1 × 26.7 mm) (NSYSU F89110402), Neimen, Kaohsiung county, coll. W.-J. Chen, 4 Nov. 2000; 2 males (largest 32.0 × 24.9 mm) (NSYSU F91050101), Lungchi, Tainan county, coll. W.-J. Chen, 1 May 2002; 2 females (largest 37.6 × 30.5 mm) (NSYSU F910222), Chishan, Kaohsiung county, coll. W.-J. Chen, 22 Feb. 2002; 1 female (31.4 × 25.0 mm) (NSYSU F920622), Tienliao, Kaohsiung county, coll. W.-J. Chen, 22 June 2003.

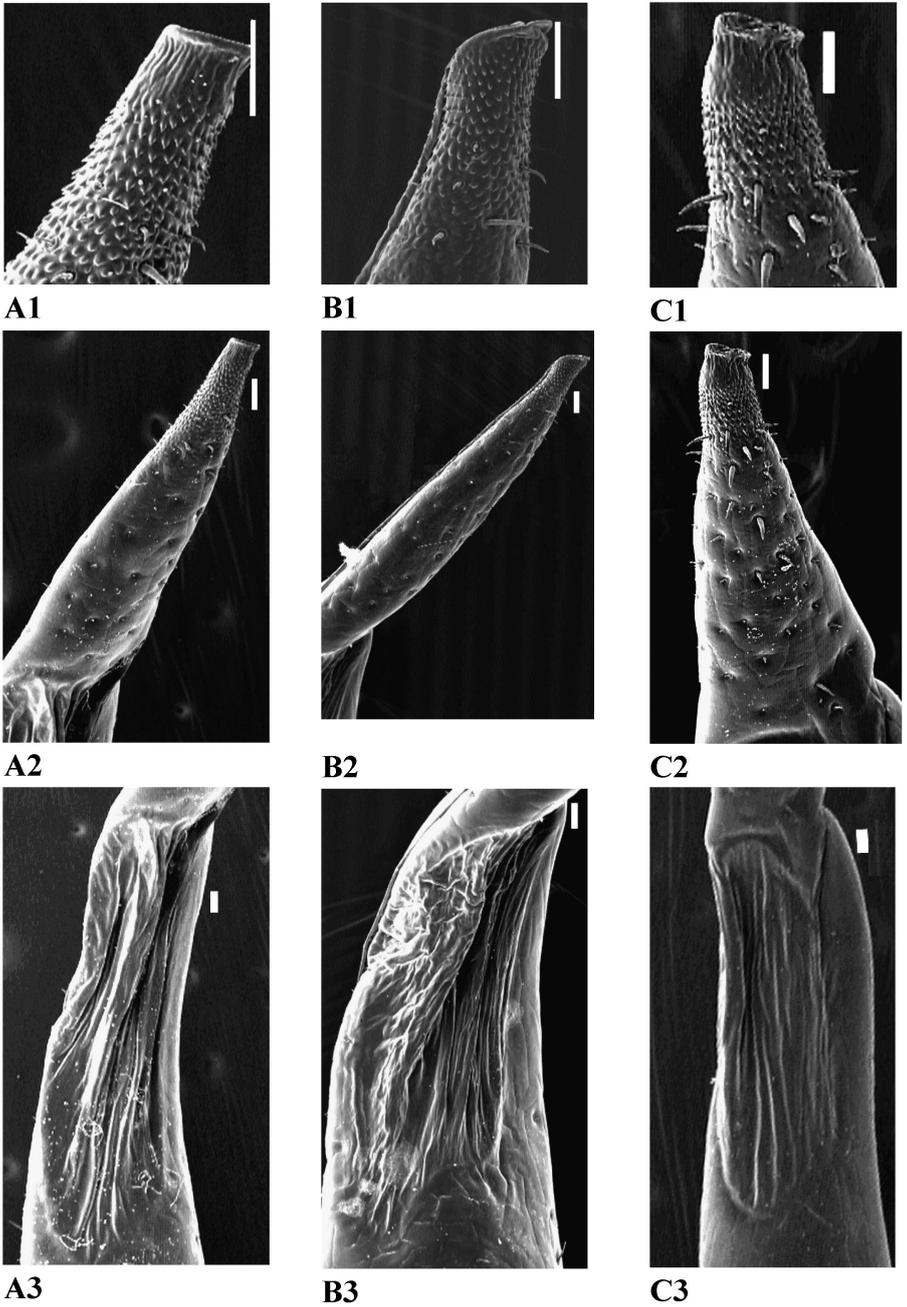


Fig. 3. Micromorphology of the right G1 of freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 by SEM. A, *G. albogilva* Shy, Ng & Yu, 1994, 29.3 × 23.8 mm (NSYSU F90121502); B, *G. ancyllophallus* Shy, Ng & Yu, 1994, 33.5 × 26.3 mm (NSYSU F89110401); C, *G. bicolor* Shy, Ng & Yu, 1994, 29.4 × 22.8 mm (NSYSU F90070301B); 1, dorsal view of terminal segment, distal part magnified; 2, dorsal view of terminal segment; 3, synovial membrane. Scales: 100  $\mu$ m.

Terminal segment. — Curved outwards and reaching slightly beyond sternal condyle in situ, distal part with 10-11 rings of scales (fig. 3B1) and a mean maximum diameter of 261.9  $\mu\text{m}$ ; dorsal aspect of terminal segment with 4 long T3 setae and 41 short T3 setae (fig. 3B2); diameter of apical opening of ejaculatory canal about 75.6  $\mu\text{m}$ ; length and width of base about 2.3 mm and 529.2  $\mu\text{m}$ , respectively.

Sub-terminal segment. — Mean width about 3.3 mm; with synovial membrane of which ratio length : width is about 2.9, basal margin low, broad, concave with a faint v-shape and top margin oblique (fig. 3B3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter 2.1-2.3  $\times$  1.8-2.0 mm, distance between pores approx. 1.6-2.1 mm.

***Geothelplusa bicolor* Shy, Ng & Yu, 1994**  
(fig. 3C1-3)

Material examined with SEM. — Male (29.4  $\times$  22.8 mm) (NSYSU F90070301B): TLG1 = 7.8 mm; AD = 85.2  $\mu\text{m}$ ; LD = 265.3  $\mu\text{m}$ ; SR = 10-11; SS = 12/34; TD = 132°; Yenping, Taitung county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2001. Male (26.0  $\times$  20.6 mm) (NSYSU F90070301), Yenping, Taitung county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2001.

Other material. — Two males, 2 females (largest female 29.4  $\times$  23.0 mm) (NSYSU F91092102), Taimali, Taitung county, coll. W.-J. Chen, 21 Sept. 2002; 1 female (31.2  $\times$  23.5 mm) (NSYSU F891114), Taimali, Taitung county, coll. W.-J. Chen, 14 Nov. 2000; 2 males, 1 female (largest male 33.2  $\times$  25.3 mm) (NSYSU F891114B), Taimali, Taitung county, coll. W.-J. Chen, 14 Nov. 2000.

Terminal segment. — Curved outwards and reaching slightly below sternal condyle in situ, distal part with 10-11 rings of scales (fig. 3C1) and a mean maximum diameter of 245.2  $\mu\text{m}$ ; dorsal aspect of terminal segment with 12 long T3 setae and 34 short T3 setae (fig. 3C2); diameter of apical opening of ejaculatory canal about 85.2  $\mu\text{m}$ ; length and width of base about 1.5 mm and 542  $\mu\text{m}$ , respectively.

Sub-terminal segment. — Mean width about 3.7 mm; with synovial membrane of which ratio length : width is about 3.5, basal margin broad, concave and top margin convex (fig. 3C3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered mainly on section 4 and more densely distributed than on outer margin, the setae of which barely reach section 4.

Female gonopores. — Diameter 3.0-3.4  $\times$  1.4-1.9 mm, distance between pores approx. 1.9-2.5 mm.

***Geothelphusa caesia* Shy, Ng & Yu, 1994**

(fig. 4A1-3)

Material examined with SEM. — Male (30.3 × 24.3 mm) (NSYSU F91052507): TLG1 = 8.4 mm; AD = 89.6 μm; LD = 242.4 μm; SR = 5-7; SS = 3/31; TD = 118°; Liukuei, Kaohsiung county, coll. W.-J. Chen, 25 May 2002; 1 male (28.7 × 22.4 mm) (NSYSU F89092301), Meinung, Kaohsiung county, coll. W.-J. Chen, 23 Sept. 2000.

Other material. — One female (37.2 × 29.9 mm) (NSYSU F89092302), Meinung, Kaohsiung county, coll. W.-J. Chen, 23 Sept. 2000; 1 male (30.2 × 23.1 mm) (NSYSU F91010501), Liukuei, Kaohsiung county, coll. W.-J. Chen, 5 Jan. 2002; 2 males (largest 29.2 × 23.2 mm) (NSYSU F9007170603), Chiahsien, Kaohsiung county, coll. W.-J. Chen, 17 July 2001; 1 male, 1 female (male 33.3 × 25.8 mm) (NSYSU F89092302), Meinung, Kaohsiung, coll. W.-J. Chen, 23 Sept. 2000.

Terminal segment. — Curved outwards and reaching below sternal condyle in situ, distal part with 5-8 rings of scales (fig. 4A1) and a mean maximum diameter of 227.9 μm; dorsal aspect of terminal segment with 3 long T3 setae and 31-32 short T3 setae (fig. 4A2); diameter of apical opening of ejaculatory canal about 89.6 μm; length and width of base about 1.6 mm and 540.5 μm, respectively.

Sub-terminal segment. — Mean width about 2.4 mm; with synovial membrane of which ratio length : width is about 3.8, base margin low, concave with a faint v-shape and top margin convex (fig. 4A3); with an indistinct protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered mainly on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach section 4.

Female gonopores. — Diameter 3.0 × 2.1-2.4 mm, distance between pores approx. 2.9 mm.

***Geothelphusa cinerea* Shy, Ng & Yu, 1994**

(fig. 4B1-3)

Material examined with SEM. — Male (29.0 × 22.9 mm) (NSYSU F90070310): TLG1 = 6.8 mm; AD = 85.5 μm; LD = 252.7 μm; SR = 8-10; SS = 5/31; TD = 101°; Lichi, Taitung county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2001; 1 male (29.4 × 23.1 mm) (NSYSU F9107010102), Lichi, Taitung county, coll. W.-J. Chen & Z.-S. Sun, 1 July 2002.

Other material. — One female (30.3 × 23.1 mm) (NSYSU F90070310), Lichi, Taitung county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2001; 2 males (largest 27.9 × 22.1 mm) (NSYSU F91020325), Kuanshan, Taitung county, coll. W.-J. Chen & Z.-S. Sun, 3 Feb. 2002; 1 male, 1 female (female 31.3 × 24.3 mm) (NSYSU F90070309B), Lichi, Taitung county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2001.

Terminal segment. — Curved outwards and reaching nearly to sternal condyle in situ, distal part with 8-10 rings of scales (fig. 4B1) and a maximum diameter of 252.7 μm; dorsal aspect of terminal segment with 5 long T3 setae and 31 short T3 setae (fig. 4B2); diameter of apical opening of ejaculatory canal about 85.5 μm; length and width of base about 1.4 mm and 545.5 μm, respectively.

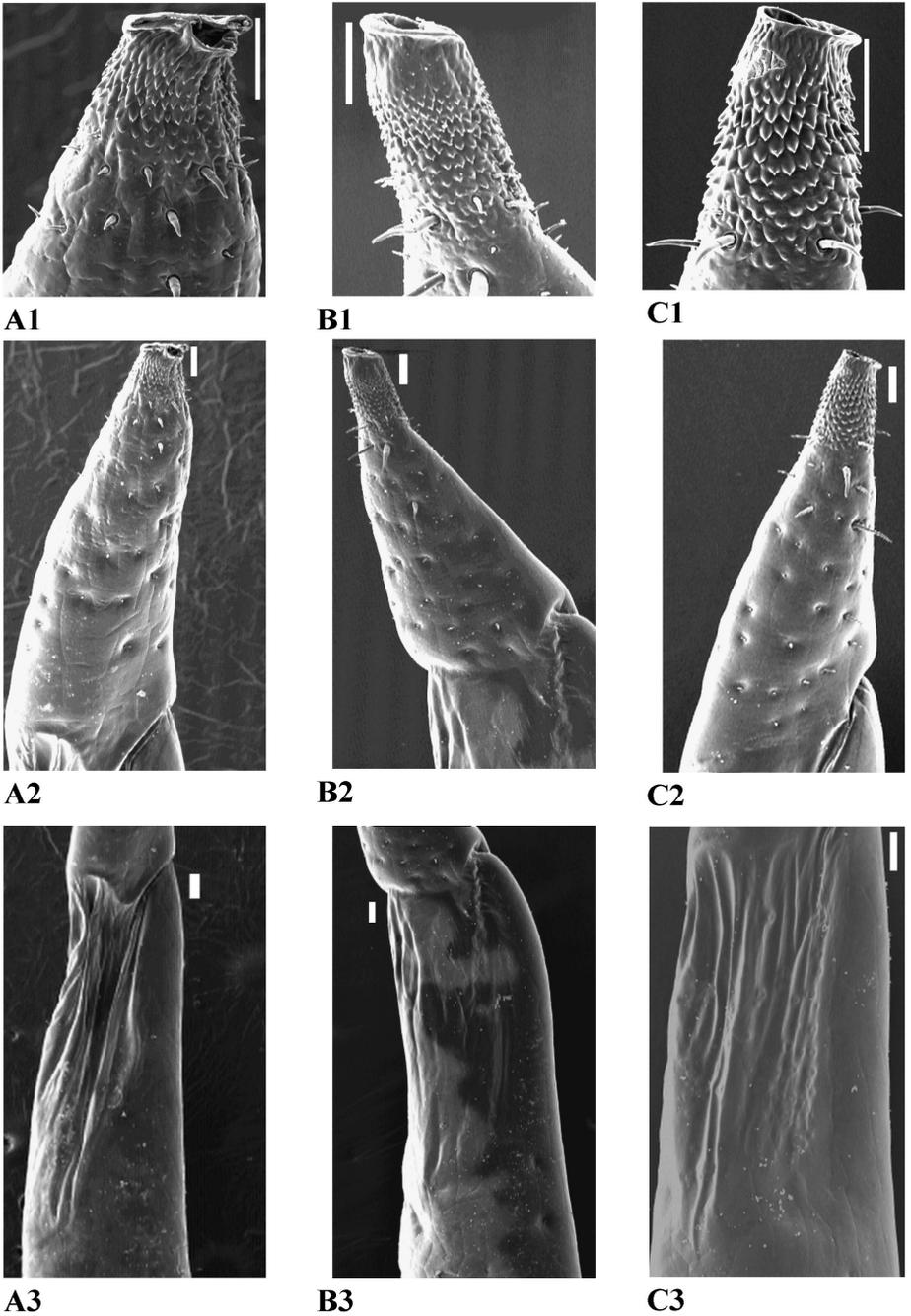


Fig. 4. Micromorphology of the right G1 of freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 by SEM. A, *G. caesia* Shy, Ng & Yu, 1994, 30.3 × 24.3 mm (NSYSU F91052507); B, *G. cinerea* Shy, Ng & Yu, 1994, 29.0 × 22.9 mm (NSYSU F90070310); C, *G. dolichopodes* Shy, Ng & Yu, 1994, 24.3 × 18.3 mm (NSYSU F89081204); 1, dorsal view of terminal segment, distal part magnified; 2, dorsal view of terminal segment; 3, synovial membrane. Scales: 100  $\mu$ m.

Sub-terminal segment. — Mean width about 2.2 mm; with synovial membrane of which ratio length : width is about 2.8, base margin broad, concave with a v-shape and top margin horizontal (fig. 4B3); with one indistinct protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered mainly on section 4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter  $3.0\text{-}3.3 \times 1.8\text{-}1.9$  mm, distance between pores approx. 1.9-2.0 mm.

### ***Geothelphusa dolichopodes* Shy, Ng & Yu, 1994**

(fig. 4C1-3)

Material examined with SEM. — Male ( $24.3 \times 18.3$  mm) (NSYSU F89081204): TLG1 = 6.1 mm; AD =  $65.8 \mu\text{m}$ ; LD =  $276.7 \mu\text{m}$ ; SR = 9-10; SS = 9/26; TD =  $125^\circ$ ; Hsiulin, Hwalien county, coll. W.-J. Chen & J.-Y. Shy, 12 Aug. 2000.

Other material. — Two males, 1 female ( $24.0 \times 18.9$  mm) (NSYSU F89081205), Hsiulin, Hwalien county, coll. W.-J. Chen & J.-Y. Shy, 12 Aug., 2000.

Terminal segment. — Curved outwards and reaching slightly below sternal condyle in situ, distal part with 9-10 rings of scales (fig. 4C1) and a mean maximum diameter of  $266.0 \mu\text{m}$ ; dorsal aspect of terminal segment with 9 long T3 setae and 26 short T3 setae (fig. 4C2); diameter of apical opening of ejaculatory canal about  $65.8 \mu\text{m}$ ; length and width of base about 1.1 mm and  $427.7 \mu\text{m}$ , respectively.

Sub-terminal segment. — Width about 1.1 mm; with synovial membrane of which ratio length : width is about 2.9, basal margin v-shape and top margin oblique (fig. 4C3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach section 4.

Female gonopores. — Diameter  $2.1\text{-}2.3 \times 1.2\text{-}1.3$  mm, distance between pores approx. 1.8 mm.

### ***Geothelphusa eucrinodonta* Shy, Ng & Yu, 1994**

(figs. 1-2)

Material examined with SEM. — Male ( $15.3 \times 11.9$  mm) (NSYSU F710041): TLG1 = 4.1 mm; AD =  $55.8 \mu\text{m}$ ; LD =  $188.3 \mu\text{m}$ ; SR = 6-8; SS = 11/18; TD =  $120^\circ$ ; Kungliao, Homei, Taipei county, coll. W.-J. Chen & C.-F. Tseng, 10 July 2003.

Other material. — One male, 1 female ( $17.5 \times 13.0$  mm) (NSYSU F81501), Kungliao, Homei, Taipei county, coll. W.-J. Chen & J.-Y. Shy, 15 Aug. 2001; 1 male, 1 female ( $23.2 \times 19.3$  mm) (NSYSU F710042), Kungliao, Homei, Taipei county, coll. W.-J. Chen & C.-F. Tseng, 10 July 2003.

Terminal segment. — Curved outwards and reaching below sternal condyle in situ, distal part with 6-8 rings of scales (fig. 2C) and a mean maximum diameter of

183.5  $\mu\text{m}$ ; dorsal aspect of terminal segment with 11 long T3 setae and 18 short T3 setae (fig. 1A); diameter of apical opening of ejaculatory canal about 55.8  $\mu\text{m}$  (fig. 1A1); length and width of base about 0.7 mm and 466.2  $\mu\text{m}$ , respectively.

Sub-terminal segment. — Width about 1.65 mm; with synovial membrane of which ratio length : width is about 3.0, basal margin v-shape and top margin horizontal (fig. 1B); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on section 4 and more densely distributed than on outer margin, the setae of which barely reach section 2 (fig. 1D-F).

Female gonopores. — Diameter 2.2-2.3  $\times$  1.5-1.6 mm, distance between pores approx. 1.5-1.9 mm.

### ***Geothelphusa eurysoma* Shy, Ng & Yu, 1994**

(fig. 5A1-3)

Material examined with SEM. — Male (21.8  $\times$  15.8 mm) (NTOU F10110), left G1: TLG1 = 4.2 mm; AD = 32.2  $\mu\text{m}$ ; LD = 225.2  $\mu\text{m}$ ; SR = 4-5; SS = 7/21; TD = 60°; Chingshan, Hoping, Taichung county, coll. J.-Y. Shy & K. Lee, 19 Oct. 1992.

Other material. — Two females (largest 19.2  $\times$  14.4 mm) (NTOU F10111), Chingshan, Hoping, Taichung county, coll. J.-Y. Shy & K. Lee, 19 Oct. 1992.

Terminal segment. — Curved inwards, distal part with 4-5 rings of scales (fig. 5A1) and a mean maximum diameter of 211.5  $\mu\text{m}$ ; dorsal aspect of terminal segment with 7 long T3 setae and 21 short T3 setae (fig. 5A2); diameter of apical opening of ejaculatory canal about 32.2  $\mu\text{m}$ ; length and width of base about 0.8 mm and 313.0  $\mu\text{m}$ , respectively.

Sub-terminal segment. — Mean width about 0.8 mm; with synovial membrane of which ratio length : width is about 2.3, basal margin low, broad, concave and top margin oblique (fig. 5A3); without conspicuous protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on section 4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter 1.5-1.7  $\times$  1.0-1.1 mm, distance between pores approx. 0.9 mm.

### ***Geothelphusa gracilipes* Shy, Ng & Yu, 1994**

(fig. 5B1-3)

Material examined with SEM. — Male (23.4  $\times$  19.0 mm) (NSYSU F7030101); TLG1 = 5.3 mm; AD = 42.9  $\mu\text{m}$ ; LD = 228.2  $\mu\text{m}$ ; SR = 7-8; SS = 9/28; TD = 118°; Hsiulin, Lushui, Hwalien county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2002; 1 male (19.12  $\times$  14.2 mm) (NSYSU F89081201), TLG1 = 5.5 mm; AD = 43.0  $\mu\text{m}$ ; LD = 152.1-189.7  $\mu\text{m}$ ; SR = 7-8; SS = 12/23; TD = 108°; Hsiulin, Lushui, Hwalien county, coll. W.-J. Chen & J.-Y. Shy, 2 Aug. 2000.

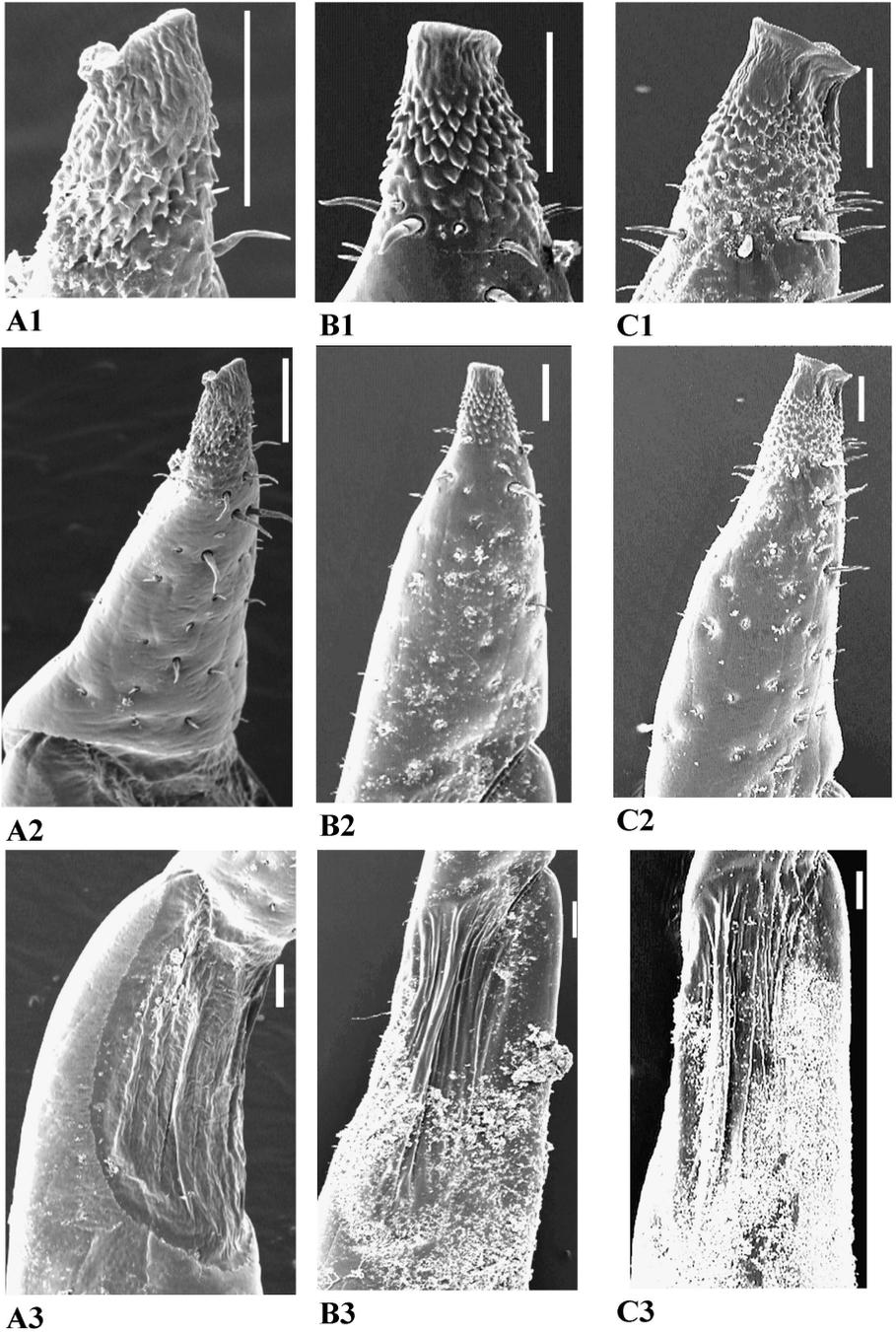


Fig. 5. Micromorphology of the right G1 of freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 by SEM. A, *G. eurysoma* Shy, Ng & Yu, 1994, 21.8 × 15.8 mm (NTOU F10110) (left G1); B, *G. gracilipes* Shy, Ng & Yu, 1994, 23.4 × 19.0 mm (NSYSU F7030101); C, *G. ilan* Shy, Ng & Yu, 1994, 26.3 × 20.9 mm (NSYSU F92022801); 1, dorsal view of terminal segment, distal part magnified; 2, dorsal view of terminal segment; 3, synovial membrane. Scales: 100  $\mu$ m.

Other material. — One male, 1 female (21.5 × 16.2 mm) (NSYSU F89081202), Hsiulin, Lushui, Hwalien county, coll. W.-J. Chen & J.-Y. Shy, 2 Aug. 2000; 1 male, 1 female (23.5 × 17.5 mm) (NSYSU F7030102), Hsiulin, Lushui, Hwalien county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2002.

Terminal segment. — Curved inwards and reaching slightly beyond sternal condyle in situ, distal part with 7-8 rings of scales (fig. 5B1) and a mean maximum diameter of 192.4  $\mu\text{m}$ ; dorsal aspect of terminal segment with 9-12 long T3 setae and 23-28 short T3 setae (fig. 5B2); diameter of apical opening of ejaculatory canal about 43  $\mu\text{m}$ ; length and width of base about 1 mm and 270  $\mu\text{m}$ , respectively.

Sub-terminal segment. — Mean width about 1.65 mm; with synovial membrane of which ratio length : width is about 3.7-5.0, basal margin in arc shape and top margin oblique (fig. 5B3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach section 3.

Female gonopores. — Diameter 2.1 × 1.1-1.4 mm, distance between pores approx. 1.1-1.6 mm.

### ***Geothelphusa ilan* Shy, Ng & Yu, 1994**

(fig. 5C1-3)

Material examined with SEM. — Male (26.3 × 20.9 mm) (NSYSU F92022801): TLG1 = 6.0 mm; AD = 76.4  $\mu\text{m}$ ; LD = 260.7  $\mu\text{m}$ ; SR = 6-7; SS = 10/36; TD = 127°; Tatung, Lunpi, Ilan county, coll. W.-J. Chen & Z.-S. Sun, 28 Feb. 2003.

Other material. — Five females (largest 28.9 × 22.8 mm) (NSYSU F90081503), Tatung, Lunpi, Ilan county, coll. W.-J. Chen & J.-Y. Shy, 15 Aug. 2001; 2 males (largest 25.1 × 19.6 mm) (NSYSU F920228012), Tatung, Insu, Ilan county, coll. W.-J. Chen & Z.-S. Sun, 28 Feb. 2003.

Terminal segment. — Curved outwards and reaching below sternal condyle in situ, distal part with 6-7 rings of scales (fig. 5C1) and a mean maximum diameter of 243.7  $\mu\text{m}$ ; dorsal aspect of terminal segment with 10 long T3 setae and 36 short T3 setae (fig. 5C2); diameter of apical opening of ejaculatory canal about 76.4  $\mu\text{m}$ ; length and width of base about 1.0 mm and 445.1  $\mu\text{m}$ , respectively.

Sub-terminal segment. — Width about 2.6 mm; with synovial membrane of which ratio length : width is about 3.2, basal margin slightly v-shape and top margin oblique (fig. 5C3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter 3.0 × 2.0 mm, distance between pores approx. 1.8 mm.

***Geothelphusa lanyu* Shy, Ng & Yu, 1994**  
(fig. 6A1-3)

Material examined with SEM. — Male (21.5 × 16.4 mm) (NSYSU F91032301): TLG1 = 5.5 mm; AD = 51.4 μm; LD = 179.4 μm; SR = 5-6, SS = 2/23; TD = 115°; Lanyu, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 23 Mar. 2002; 1 male (17.8 × 13.5 mm) (NSYSU F9103221), Lanyu, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 22 Mar. 2002.

Other material. — One male, 4 females (largest female 20.1 × 15.6 mm) (NSYSU F910322011), Lanyu, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 22 Mar. 2002; 1 female (16.9 × 13.0 mm) (NSYSU F910322), Lanyu, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 22 Mar. 2002; 4 males (largest 17.6 × 14.0 mm) (NSYSU F91032302), Lanyu, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 23 Mar. 2002.

Terminal segment. — Curved outwards and reaching beyond sternal condyle in situ, distal part with 5-6 rings of scales (fig. 6A1) and a mean maximum diameter of 172.2 μm; dorsal aspect of terminal segment with 2 long T3 setae and 23 short T3 setae (fig. 6A2); diameter of apical opening of ejaculatory canal about 51.4 μm; length and width of base about 1.0 mm and 393.3 μm, respectively.

Sub-terminal segment. — Width about 2.0 mm; with synovial membrane of which ratio length : width is about 3.0, basal margin a faint v-shape and top margin concave (fig. 6A3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach section 3.

Female gonopores. — Diameter 2.0 × 1.8-1.9 mm, distance between pores approx. 1.0 mm.

***Geothelphusa lutao* Shy, Ng & Yu, 1994**  
(fig. 6B1-3)

Material examined with SEM. — Male (22.3 × 17.4 mm) (NSYSU F91112301): TLG1 = 5.5 mm; AD = 68.2 μm; LD = 229.4 μm; SR = 5-7; SS = 4/34; TD = 115°; Lutao, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 23 Nov. 2002.

Other material. — Nine males, 1 female (19.6 × 14.6 mm) (NSYSU F91112302), Lutao, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 23 Nov. 2002.

Terminal segment. — Curved outwards and reaching below sternal condyle in situ, distal part with 5-7 rings of scales (fig. 6B1) and a mean maximum diameter of 221.5 μm; dorsal aspect of terminal segment with 4 long T3 setae and 34 short T3 setae (fig. 6B2); diameter of apical opening of ejaculatory canal about 68.2 μm; length and width of base about 1.1 mm and 467.1 μm, respectively.

Sub-terminal segment. — Width about 2.3 mm; with synovial membrane of which ratio length : width is about 2.7, basal margin concave and a faint v-shape and top margin horizontal (fig. 6B3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin

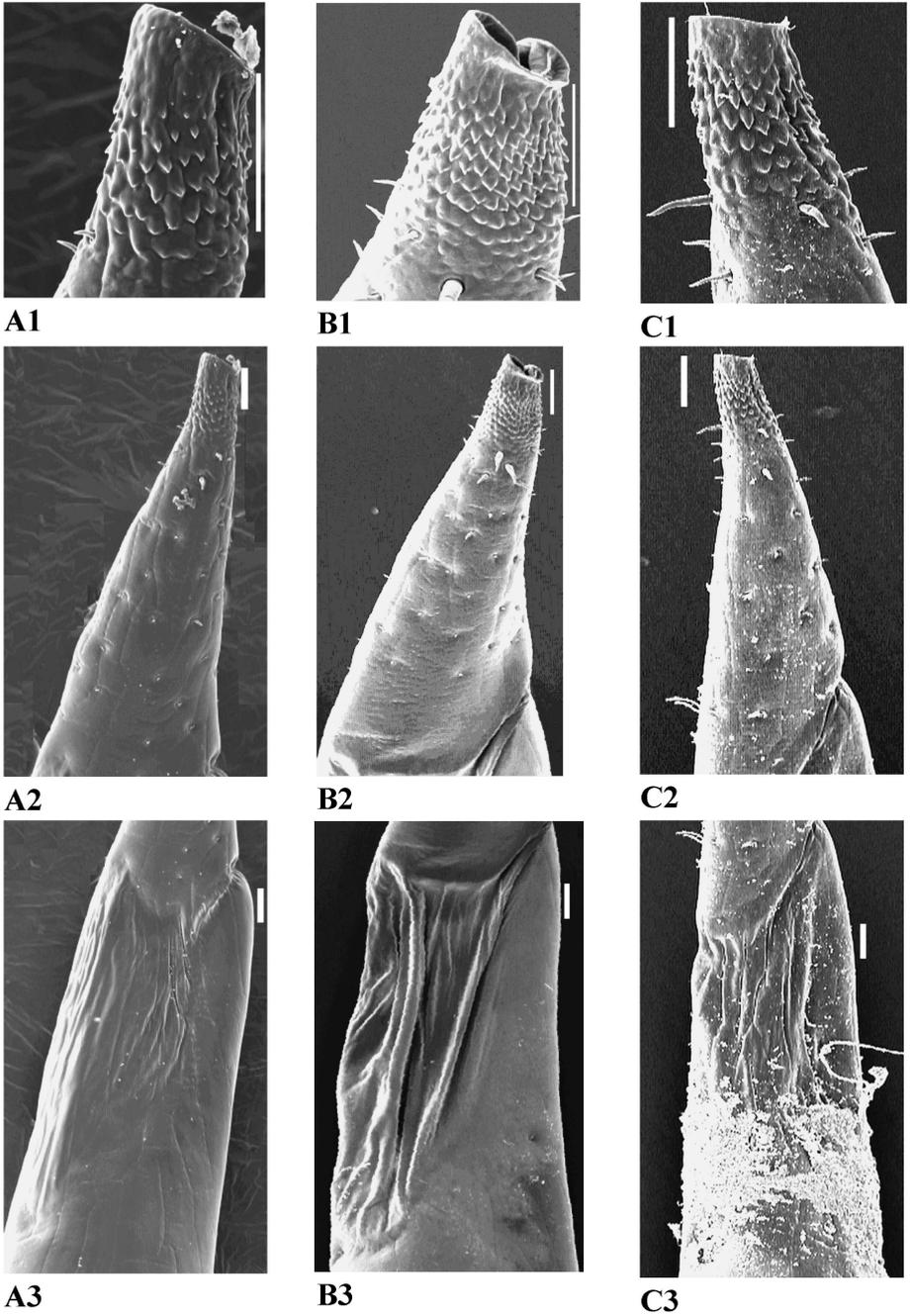


Fig. 6. Micromorphology of the right G1 of freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 by SEM. A, *G. lanyu* Shy, Ng & Yu, 1994, 21.5 × 16.4 mm (NSYSU F91032301); B, *G. lutoa* Shy, Ng & Yu, 1994, 22.3 × 17.4 mm (NSYSU F91112301); C, *G. monticola* Shy, Ng & Yu, 1994, 18.3 × 14.1 mm (NSYSU F92030104); 1, dorsal view of terminal segment, distal part magnified; 2, dorsal view of terminal segment; 3, synovial membrane. Scales: 100 μm.

with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter  $1.5\text{-}1.9 \times 1.0\text{-}1.1$  mm, distance between pores approx. 1.1 mm.

***Geothelphusa monticola* Shy, Ng & Yu, 1994**

(fig. 6C1-3)

Material examined with SEM. — Male ( $18.3 \times 14.1$  mm) (NSYSU F92030104): TLG1 = 4.7 mm; AD =  $51.7 \mu\text{m}$ ; LD =  $180.6 \mu\text{m}$ ; SR = 4-5; SS = 4/19; TD =  $102^\circ$ ; Hoping, Songmao, Taichung county, coll. W.-J. Chen & Z.-S. Sun, 1 Mar. 2003.

Other material. — One male ( $20.64 \times 16.12$  mm) (NTOU F10112), Hoping, Sheauyeakow, Taichung county, coll. J.-Y. Shy & W.-L. Tsay, 28 June 1993; 1 male 1 female (NSYSU F92030103), Hoping, Siyuan, Taichung county, coll. W.-J. Chen & Z.-S. Sun, 1 Mar. 2003; 3 males, 1 female ( $17.1 \times 14.3$  mm) (NSYSU F93111301), Lishan, Taichung county, coll. W.-J. Chen & C.-F. Tseng, 13 Nov. 2004.

Terminal segment. — Curved outwards and reaching slightly beyond sternal condyle in situ, distal part with 4-5 rings of scales (fig. 6C1) and a mean maximum diameter of  $169.9 \mu\text{m}$ ; dorsal aspect of terminal segment with 4 long T3 setae and 19 short T3 setae (fig. 6C2); diameter of apical opening of ejaculatory canal about  $51.7 \mu\text{m}$ ; length and width of base about 1.0 mm and  $298.8 \mu\text{m}$ , respectively.

Sub-terminal segment. — Width about 2.1 mm; with synovial membrane of which ratio length : width is about 2.8, basal margin low, narrow, concave and top margin oblique (fig. 6C3); with one low protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter  $2.0 \times 0.9$  mm, distance between pores approx. 1.3 mm.

***Geothelphusa nanao* Shy, Ng & Yu, 1994**

(fig. 7A1-3)

Material examined with SEM. — Male ( $30.2 \times 23.3$  mm) (NSYSU F0815042): TLG1 = 7.6 mm; AD =  $90.1 \mu\text{m}$ ; LD =  $270.1 \mu\text{m}$ ; SR = 8-9, SS = 3/27; TD =  $98^\circ$ ; Nanao, Chinyang, Ilan county, coll. W.-J. Chen & J.-Y. Shy, 15 Aug. 2001.

Other material. — Two males, 5 females (largest female  $25.9 \times 20.0$  mm) (NSYSU F90081504), Nanao, Chinyang, Ilan county, coll. W.-J. Chen & J.-Y. Shy, 15 Aug. 2001.

Terminal segment. — Curved outwards and reaching below sternal condyle in situ, distal part with 8-9 rings of scales (fig. 7A1) and a maximum diameter of  $270.1 \mu\text{m}$ ; dorsal aspect of terminal segment with 3 long T3 setae and 27 short T3 setae (fig. 7A2); diameter of apical opening of ejaculatory canal about  $90.1 \mu\text{m}$ ; length and width of base about 0.9 mm and  $506.1 \mu\text{m}$ , respectively.

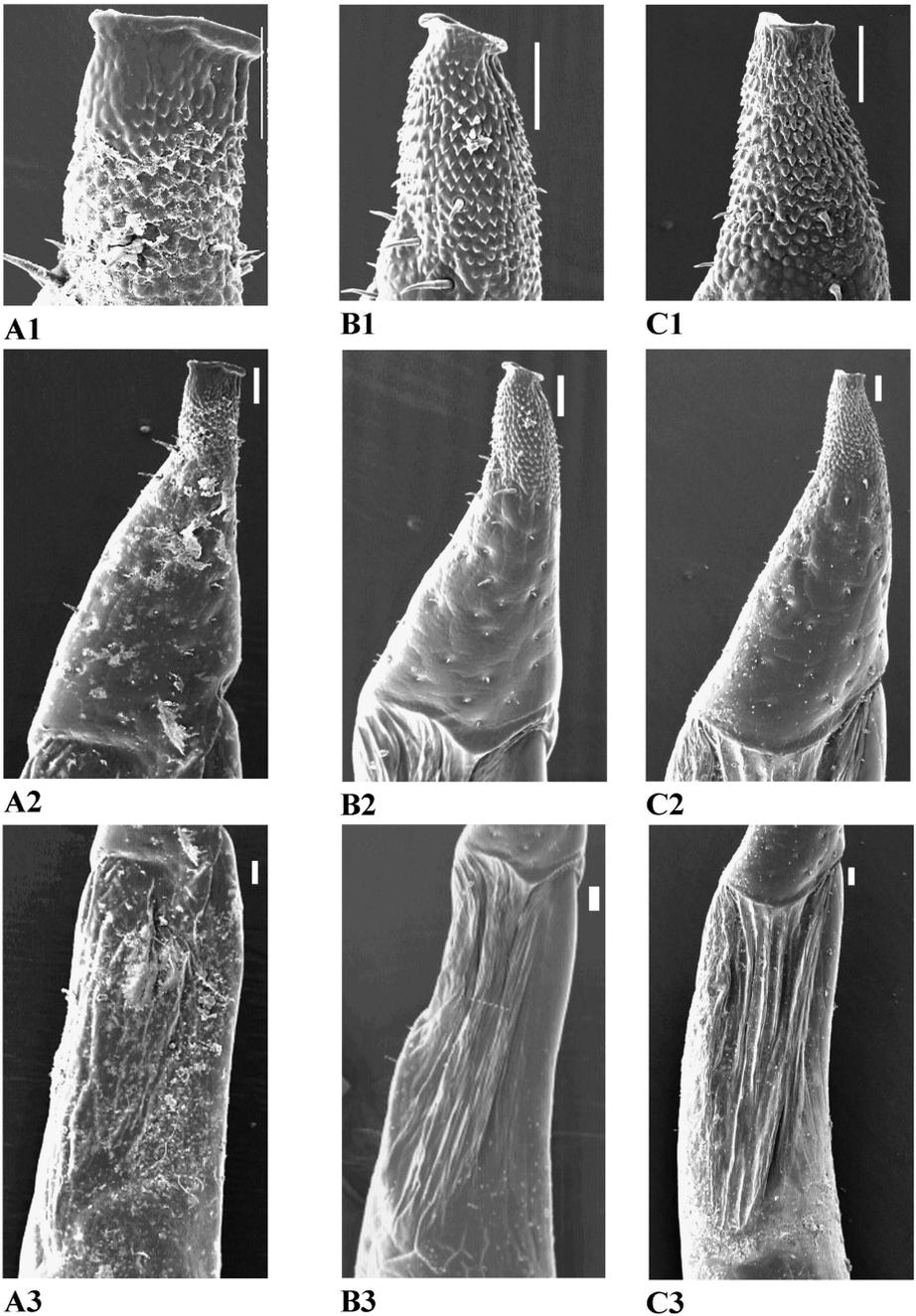


Fig. 7. Micromorphology of the right G1 of freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 by SEM. A, *G. nanao* Shy, Ng & Yu, 1994, 30.2 × 23.3 mm (NSYSU F0815042); B, *G. nanhsi* Shy, Ng & Yu, 1994, 25.2 × 20.3 mm (NSYSU F89110401); C, *G. olea* Shy, Ng & Yu, 1994, 30.6 × 24.1 mm (NSYSU F90102202); 1, dorsal view of terminal segment, distal part magnified; 2, dorsal view of terminal segment; 3, synovial membrane. Scales: 100  $\mu$ m.

Sub-terminal segment. — Width about 2.7 mm; with synovial membrane of which ratio length : width is about 3.5, basal margin v-shape and top margin horizontal (fig. 7A3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter  $2.5 \times 1.5$ -1.6 mm, distance between pores approx. 1.1-1.2 mm.

### ***Geothelphusa nanhsi* Shy, Ng & Yu, 1994**

(fig. 7B1-3)

Material examined with SEM. — Male (25.2  $\times$  20.3 mm) (NSYSU F89110401): TLG1 = 7.3 mm; AD = 67.7  $\mu$ m; LD = 181.6  $\mu$ m; SR = 14-15; SS = 5/27; TD = 128°; Neimen, Kaohsiung county, coll. W.-J. Chen, 4 Nov. 2000; 1 male (23.3  $\times$  18.3 mm) (NTOU F10198), Nanhsi, Tainan county, coll. J.-Y. Shy & W.-L. Tsay, 7 Aug. 1992.

Other material. — Two males, 1 female (female 29.8  $\times$  23.2 mm) (NSYSU F93112104), Nanhsi, Tainan county, coll. W.-J. Chen, 21 Nov. 2004; 3 males (largest 26.2  $\times$  21.0 mm) (NSYSU F91102605), Nanhsi, Tainan county, coll. W.-J. Chen, 26 Oct. 2002; 1 male, 1 female (female 29.8  $\times$  23.2 mm) (NSYSU F91051106), Nanhsi, Tainan county, coll. W.-J. Chen, 11 May 2002.

Terminal segment. — Curved outwards and reaching beyond sternal condyle in situ, distal part with 14-17 rings of scales (fig. 7B1) and a mean maximum diameter of 178.8  $\mu$ m; dorsal aspect of terminal segment with 5 long T3 setae and 27 short T3 setae (fig. 7B2); diameter of apical opening of ejaculatory canal about 67.7  $\mu$ m; length and width of base about 1.1 mm and 487.5  $\mu$ m, respectively.

Sub-terminal segment. — Mean width about 2.3 mm; with synovial membrane of which ratio length : width is about 4.4, basal margin low, concave and top margin slightly convex (fig. 7B3); with one faint protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered mainly on section 4 and more densely distributed than on outer margin, the setae of which barely reach section 4.

Female gonopores. — Diameter 2.8-3.3  $\times$  1.8-2.0 mm, distance between pores approx. 1.4-1.8 mm.

### ***Geothelphusa olea* Shy, Ng & Yu, 1994**

(fig. 7C1-3)

Material examined with SEM. — Male (30.6  $\times$  24.1 mm) (NSYSU F90102202): TLG1 = 7.2 mm; AD = 68.7  $\mu$ m; LD = 274.8  $\mu$ m; SR = 10-11; SS = 3/29, TD = 126°; Paiho, Tainan county, coll. W.-J. Chen, 22 Oct. 2001.

Other material. — One male, 2 females (largest female 38.1  $\times$  30.1 mm) (NSYSU F91102602), Paiho, Tainan county, coll. W.-J. Chen, 26 Oct. 2002; 1 male, 1 female (female 36.2  $\times$  28.2 mm) (NSYSU F91102604), Tungshan, Tainan county, coll. W.-J. Chen, 26 Oct. 2002; 4 males (largest

27.4 × 22.1 mm) (NSYSU F91100102), Nanhsi, Tainan county, coll. W.-J. Chen, 1 Oct. 2002; 2 males (largest 32.8 × 25.9 mm) (NSYSU F91122202), Yuching, Tainan county, coll. W.-J. Chen, 22 Dec. 2002.

**Terminal segment.** — Curved outwards and reaching below sternal condyle in situ, distal part with 10-11 rings of scales (fig. 7C1) and a mean maximum diameter of 261.5 μm; dorsal aspect of terminal segment with 3 long T3 setae and 29 short T3 setae (fig. 7C2); diameter of apical opening of ejaculatory canal about 68.7 μm; length and width of base about 1.4 mm and 570.4 μm, respectively.

**Sub-terminal segment.** — Width about 3.1 mm; with synovial membrane of which ratio length : width is about 2.8, basal margin low, concave and top margin convex (fig. 7C3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered mainly on section 4 and more densely distributed than on outer margin, the setae of which barely reach section 4.

**Female gonopores.** — Diameter 3.0-3.4 × 2.0-2.4 mm, distance between pores approx. 1.8-2.0 mm.

### ***Geothelphusa takuan* Shy, Ng & Yu, 1994**

(fig. 8A1-3)

**Material examined with SEM.** — Male (17.4 × 13.0 mm) (NSYSU F92070902): TLG1 = 4.6 mm; AD = 43.8 μm; LD = 221.3 μm; SR = 6-7; SS = 13/20; TD = 60°; Fuhsing, Takuan, Taoyuan county, coll. W.-J. Chen & C.-F. Tseng, 9 July 2003.

**Other material.** — Three males (largest 16.4 × 12.5 mm) (NSYSU F92070921), Fuhsing, Takuan, Taoyuna county, coll. W.-J. Chen & C.-F. Tseng, 9 July 2003; 3 males 4 females (largest female 21.3 × 16.1 mm) (NSYSU F92022906), Tatung, Mingchi, Ilan county, coll. W.-J. Chen & Z.-S. Sun, 29 Feb. 2003.

**Terminal segment.** — Curved inwards and reaching beyond sternal condyle in situ, distal part with 6-7 rings of scales (fig. 8A1) and a mean maximum diameter of 210.8 μm; dorsal aspect of terminal segment with 13 long T3 setae and 20 short T3 setae (fig. 8A2); diameter of apical opening of ejaculatory canal about 43.8 μm; length and width of base about 0.8 mm and 341.7 μm, respectively.

**Sub-terminal segment.** — Width about 1.9 mm; with synovial membrane of which ratio length : width is about 2.9, basal margin low, broad, concave and top margin horizontal (fig. 8A3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on section 4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

**Female gonopores.** — Diameter 2.0-2.1 × 0.9-1.0 mm, distance between pores approx. 1.2 mm.

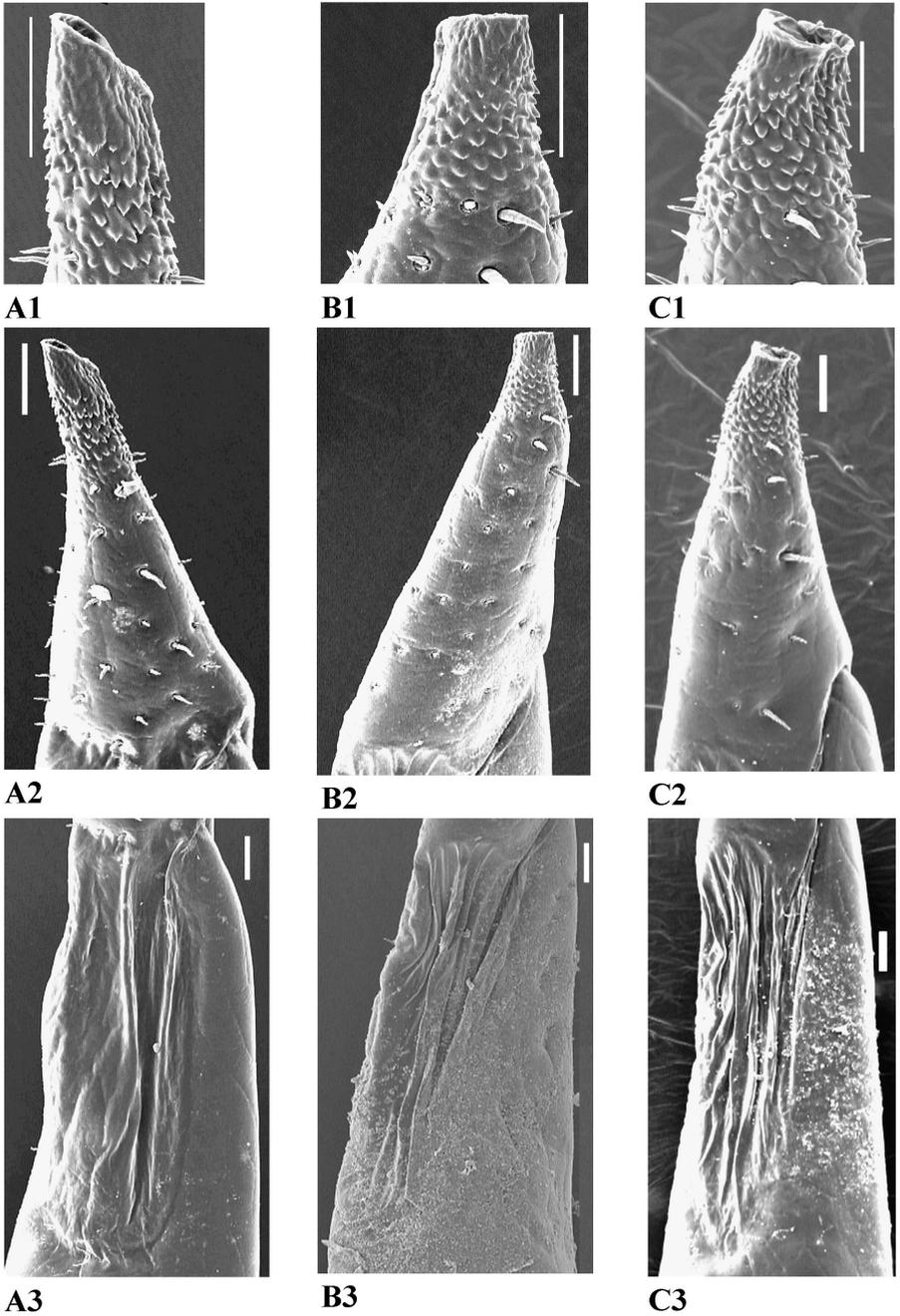


Fig. 8. Micromorphology of the right G1 of freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 by SEM. A, *G. takuan* Shy, Ng & Yu, 1994, 17.4 × 13.0 mm (NSYSU F92070902); B, *G. tali* Shy, Ng & Yu, 1994, 18.6 × 14.3 mm (NSYSU F7100301); C, *G. taroko* Shy, Ng & Yu, 1994, 20.6 × 15.6 mm (NSYSU F89081206); 1, dorsal view of terminal segment, distal part magnified; 2, dorsal view of terminal segment; 3, synovial membrane. Scales: 100  $\mu$ m.

***Geothelphusa tali* Shy, Ng & Yu, 1994**

(fig. 8B1-3)

Material examined with SEM. — Male (18.6 × 14.3 mm) (NSYSU F7100301): TLG1 = 4.4 mm; AD = 41.1 μm; LD = 146.5 μm; SR = 5-6; SS = 3/30; TD = 80°; Tali, Ilan county, coll. W.-J. Chen & C.-F. Tseng, 10 July 2003.

Other material. — One male, 3 females (largest female 23.1 × 18.0 mm) (NSYSU F7100302), Tali, Ilan county, coll. W.-J. Chen & C.-F. Tseng, 10 July 2003.

Terminal segment. — Curved outwards and reaching below sternal condyle in situ, distal part with 5-6 rings of scales (fig. 8B1) and a mean maximum diameter of 145.4 μm; dorsal aspect of terminal segment with 3 long T3 setae and 30 short T3 setae (fig. 8B2); diameter of apical opening of ejaculatory canal about 41 μm; length and width of base about 0.9 mm and 275.7 μm, respectively.

Sub-terminal segment. — Mean width about 1.4 mm; with synovial membrane of which ratio length : width is about 3.9, basal margin oblong and top margin curved (fig. 8B3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, of which setae barely reach section 4.

Female gonopores. — Diameter 1.7-2.7 × 1-1.8 mm, distance between pores approx. 1.0-1.7 mm.

***Geothelphusa taroko* Shy, Ng & Yu, 1994**

(fig. 8C1-3)

Material examined with SEM. — Male (20.6 × 15.6 mm) (NSYSU F89081206): TLG1 = 4.9 mm; AD = 70.4 μm; LD = 195.0 μm; SR = 6-8; SS = 6/17; TD = 112°; Hsiulin, Hwalien county, coll. W.-J. Chen & J.-Y. Shy, 12 Aug. 2000; 1 male (23.2 × 17.7 mm) (NSYSU F91070303): TLG1 = 5.7 mm; AD = 66.0 μm; LD = 228.1 μm; SR = 7-7; SS = 8/13; TD = 109°; Hsiulin, Lushui, Hwalien county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2002.

Other material. — Two females (largest 26.0 × 19.3 mm) (NSYSU F89081206), Hsiulin, Hwalien county, coll. W.-J. Chen & J.-Y. Shy, 12 Aug. 2000; 2 males, 4 females (largest female 26.7 × 20.9 mm) (NSYSU F91070302), Hsiulin, Lushui, Hwalien county, coll. W.-J. Chen & Z.-S. Sun, 3 July 2002.

Terminal segment. — Curved outwards and reaching slightly below sternal condyle in situ, distal part with 6-8 rings of scales (fig. 8C1) and a mean maximum diameter of 194.7 μm; dorsal aspect of terminal segment with 6-8 long T3 setae and 13-19 short T3 setae (fig. 8C2); mean diameter of apical opening of ejaculatory canal about 66.4 μm; length and width of base about 0.75 mm and 254.5 μm, respectively.

Sub-terminal segment. — Mean width about 1.83 mm; with synovial membrane of which ratio length : width is about 4.2-4.3, basal margin v-shape and top margin convex (fig. 8C3); with one protuberance on proximal outer angle. Proximal

margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on section 4 and more densely distributed than on outer margin, the setae of which barely reach section 4.

Female gonopores. — Diameter  $2.1-2.9 \times 1.6-1.7$  mm, distance between pores approx. 1.7 mm.

### ***Geothelphusa tawu* Shy, Ng & Yu, 1994**

(fig. 9A1-3)

Material examined with SEM. — Male ( $19.9 \times 15.8$  mm) (NSYSU F89081137): TLG1 = 5.3 mm; AD =  $52.1 \mu\text{m}$ ; LD =  $175 \mu\text{m}$ ; SR = 5-6, SS = 5/23, TD =  $131^\circ$ ; Tajen, Taitung county, coll. W.-J. Chen & J.-Y. Shy, 11 Aug. 2000; 1 male ( $19.2 \times 15.0$  mm) (NSYSU F89081175), Tajen, Taitung county, coll. W.-J. Chen & J.-Y. Shy, 11 Aug. 2000.

Other material. — One male, 2 females (largest female  $18.3 \times 14.8$  mm) (NSYSU F92022701), Tajen, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 27 Feb. 2003; 3 males (largest  $16.7 \times 13.6$  mm) (NSYSU F891114), Tajen, Taitung county, coll. W.-J. Chen & C.-F. Tseng, 14 Nov. 2000.

Terminal segment. — Curved outwards and reaching slightly below sternal condyle in situ, distal part with 5-6 rings of scales (fig. 9A1) and a mean maximum diameter of  $175 \mu\text{m}$ ; dorsal aspect of terminal segment with 5 long T3 setae and 23 short T3 setae (fig. 9A2); diameter of apical opening of ejaculatory canal about  $52.1 \mu\text{m}$ ; length and width of base about 1.0 mm and  $406.0 \mu\text{m}$ , respectively.

Sub-terminal segment. — Width about 1.6 mm; with synovial membrane of which ratio length : width is about 2.7, basal margin broad, v-shape and top margin slightly oblique (fig. 9A3); with one protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter  $1.6-1.9 \times 0.9-1.0$  mm, distance between pores approx. 1.1-1.4 mm.

### ***Geothelphusa tsayae* Shy, Ng & Yu, 1994**

(fig. 9B1-3)

Material examined with SEM. — Male ( $21.7 \times 17$  mm) (NSYSU F890923A2): TLG1 = 5.4 mm; AD =  $48.4 \mu\text{m}$ ; LD =  $159.4 \mu\text{m}$ ; SR = 10-11; SS = 3/19; TD =  $124^\circ$ ; Meinung, Kaohsiung county, coll. W.-J. Chen, 23 Sept. 2000; 1 male ( $27.8 \times 21.9$  mm) (NSYSU F91051905), Liukuei, Kaohsiung county, coll. W.-J. Chen, 19 May 2002.

Other material. — One male ( $24.6 \times 18.9$  mm), 1 female ( $29.6 \times 23.2$  mm) (NSYSU F93092502), Sanmin, Kaohsiung county, coll. W.-J. Chen, 25 Sept. 2004; 1 male ( $21.5 \times 18.6$  mm) (NSYSU F890923A1), Meinung, Kaohsiung county, coll. W.-J. Chen, 23 Sept. 2000; 5 males (largest  $27.9 \times 21.7$  mm) (NSYSU F91052508), Liukuei, Kaohsiung county, coll. W.-J. Chen, 25 May 2002.

Terminal segment. — Curved outwards and reaching slightly below sternal condyle in situ, distal part with 10-11 rings of scales (fig. 9B1) and a mean

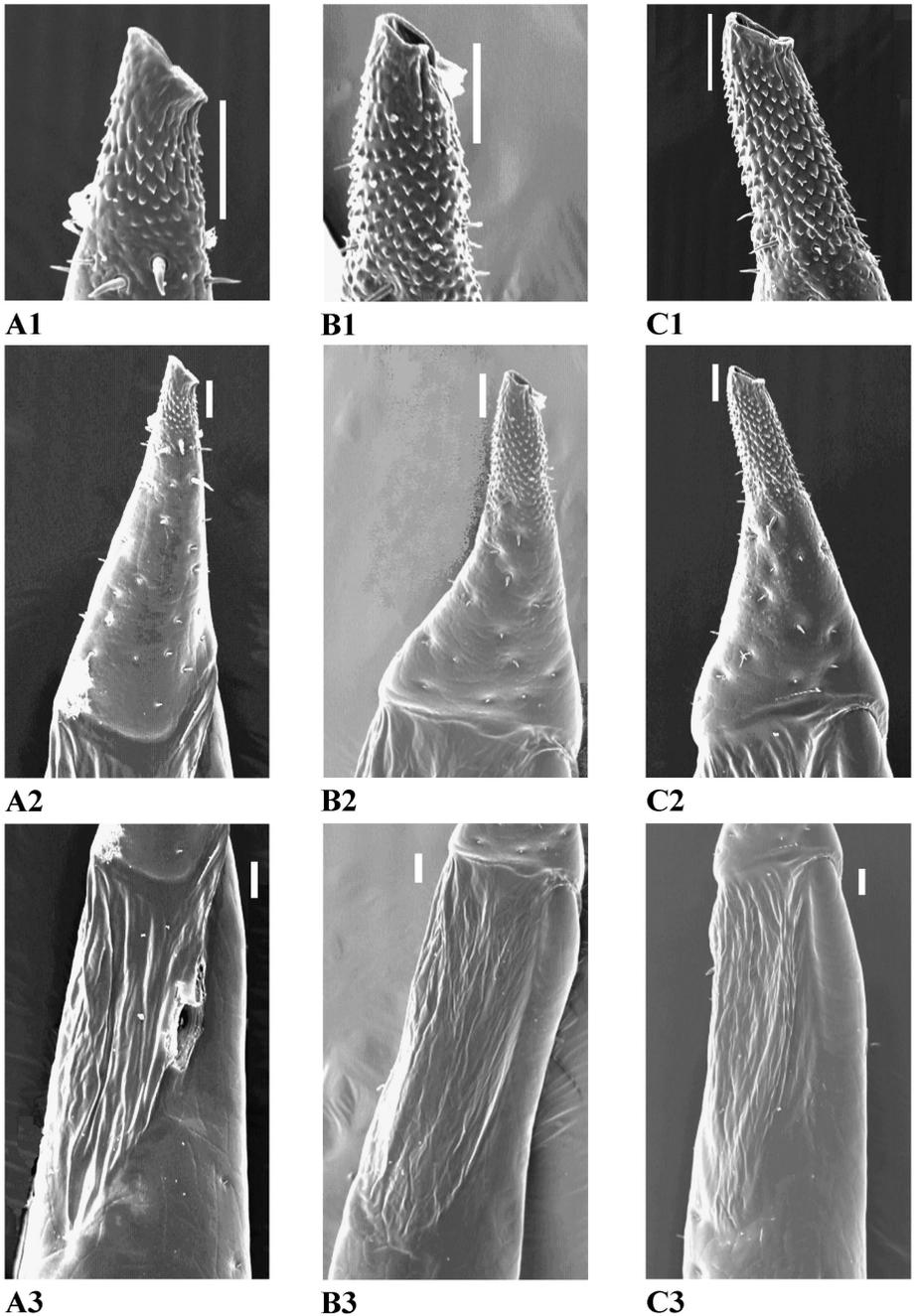


Fig. 9. Micromorphology of the right G1 of freshwater crabs of the genus *Geothelphusa* Stimpson, 1858 by SEM. A, *G. tawu* Shy, Ng & Yu, 1994, 19.9 × 15.8 mm (NSYSU F89081137); B, *G. tsayae* Shy, Ng & Yu, 1994, 21.7 × 17.0 mm (NSYSU F890923A2); C, *G. wutai* Shy, Ng & Yu, 1994, 23.3 × 18.8 mm (NTOU 10081); 1, dorsal view of terminal segment, distal part magnified; 2, dorsal view of terminal segment; 3, synovial membrane. Scales: 100  $\mu$ m.

maximum diameter of 148.9  $\mu\text{m}$ ; dorsal aspect of terminal segment with 3 long T3 setae and 19 short T3 setae (fig. 9B2); diameter of apical opening of ejaculatory canal about 48.4  $\mu\text{m}$ ; length and width of base about 0.8 mm and 451.2  $\mu\text{m}$ , respectively.

Sub-terminal segment. — Mean width about 1.8 mm; with synovial membrane of which ratio length : width about 3.7, basal margin broad, concave and top margin horizontal (fig. 9B3); with one faint protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered mainly on section 4 and more densely distributed than on outer margin, the setae of which barely reach sections 3-4.

Female gonopores. — Diameter 2.6-2.7  $\times$  1.5 mm, distance between pores approx. 1.5 mm.

### ***Geothelphusa wutai* Shy, Ng & Yu, 1994**

(fig. 9C1-3)

Material examined with SEM. — Male (23.3  $\times$  18.8 mm) (NTOU 10081): TLG1 = 7.5 mm; AD = 55.3  $\mu\text{m}$ ; LD = 188.5  $\mu\text{m}$ ; SR = 11-11; SS = 2/22; TD = 137°; Wutai, Ila, Pingtung county, coll. H.-P. Yu, 12 July 1982.

Other material. — Five males (largest 19.0  $\times$  15.3 mm), 10 females (largest 20.2  $\times$  16.0 mm) (NTOU F10081), Wutai, Ila, Pingtung county, coll. H.-P. Yu, 12 July 1982.

Terminal segment. — Curved outwards and reaching beyond sternal condyle in situ, distal part with 11 rings of scales (fig. 9C1) and a maximum diameter of 188.5  $\mu\text{m}$ ; dorsal aspect of terminal segment with 2 long T3 setae and 22 short T3 setae (fig. 9C2); diameter of apical opening of ejaculatory canal about 55.3  $\mu\text{m}$ ; length and width of base about 0.9 mm and 484.3  $\mu\text{m}$ , respectively.

Sub-terminal segment. — Mean width about 1.8 mm; with synovial membrane of which ratio length : width is about 4.0, basal margin low, broad, concave and top margin horizontal (fig. 9C3); with one faint protuberance on proximal outer angle. Proximal margin and base of sub-terminal segment with setae, inner margin with T4 setae clustered on sections 3-4 and more densely distributed than on outer margin, the setae of which barely reach section 4.

Female gonopores. — Diameter 1.9  $\times$  1.0 mm, distance between pores approx. 1.5 mm.

### DISCUSSION

The analysis of micromorphological structures of taxonomically important characters can help discriminate between species and may also contribute to our understanding of evolutionary pathways (Nielsen, 1998). In the present study, we selected 22 species of common freshwater crabs from Taiwan belonging to the

genus *Geothelphusa* for examining the G1 with SEM. The detailed morphology of the G1 of these species is described above. For a more convenient comparison of the differences in the G1 between species, the main characteristics and ratios of measurements are provided also in table I. According to Shy (1994), adult male *Geothelphusa* had been divided into three body-size groups according to carapace width. We found as major differences between these three body-size groups the scattered setae (SS) as well as the rings of scales (SR) on the terminal segment of G1. Crabs of group L have specifically higher numbers than those of group S. The length of the terminal segment of G1 is less in group M, and the shortest length occurs in individuals of *G. dolichopodes*, *G. nanao*, and *G. wutai* (table I).

The direction of the curve of the tip of G1 (TD) in ventral view, relative to the terminal segment, mostly has an angle greater than 95°, defined as curved outwards, except in *G. takuan*, *G. eurysoma*, and *G. tali*, where the tip is curved inwards. In Shy et al. (1994), the tips of *G. olea*, *G. nanhsi*, *G. wutai*, *G. tsayae*, *G. bicolor*, and *G. lanyu* were described as slightly curved inwards, too. We suggest these differences result from the way of taking the measurements, where we examined the tip at the apical opening of the ejaculatory canal, whereas the curve direction of the terminal segment was used by Shy et al. (1994).

The synovial membrane on G1 could be a key characteristic to discriminate between species. In 1995, a new genus, *Ryukyum* Ng & Shokita, 1995 (Potamidae) was established for the terrestrial potamid crab from the Ryukyu Islands, and as one of the important characteristics the authors used in the structure of G1, which had a synovial membrane (Ng & Shokita, 1995). The presence of a well developed synovial membrane was mentioned as the main difference between the genera *Ryukyum* and *Nanhaipotamon*, as the latter lacked it (Ng & Shokita, 1995). In the present study, the genus *Geothelphusa* is also shown to have a well developed synovial membrane on G1, and its micromorphology varies among species. For instance, *G. tawu*, *G. lanyu*, and *G. lutao* could easily be distinguished by the top margin of their synovial membrane. Furthermore, by comparison of the G1 under SEM, there are other differences among these three species, i.e., scattered setae, rings of scales, and the TLG1/SW ratio (table I). This despite the fact that Shih et al. (2004) used molecular methods to assess the systematics of a part of the southern Taiwanese *Geothelphusa* species, and suggested *G. lanyu*, *G. lutao*, and *G. tawu* could be conspecific. We assume that the variations in the micromorphology of the reproductive organs may have resulted in reproductive isolation as at step 2 of the allopatric model (Grant & Grant, 1996). Reinforcement of the speciation process may also have been accomplished through various ecological pressures, or from a degree of reproductive incompatibility rather recently (Liou & Price, 1994; Grant & Grant, 1996; Schluter, 1996; Rundle & Schluter, 1998; Servedio, 2000). The above results could hence support the taxonomic system of Shy et al. (1994) and that of Ng et al. (2001), too.

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