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Taxonomy of the Terrestrial Crab *Geothelphusa tenuimanus* (Crustacea: Decapoda: Brachyura: Potamidae) of Okinawa Island, Central Ryukyus, Japan

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The Okinawan terrestrial crab *Geothelphusa tenuimanus* is redescribed and its intraspecific variation is discussed. The geographically isolated Tamagusuku (=southern) population tends to have a more laterally-directed curvature of the anterolateral margins of the carapace and relatively shorter fourth ambulatory legs. However, these differences are not very significant and the diagnostic male first gonopod shows no differences. Therefore, all the populations on Okinawa Island are here regarded as conspecific. Habitats and morphological adaptations of the species are also discussed.
Key Words: *Geothelphusa tenuimanus*, taxonomy, redescription, Potamidae, terrestrial crab.

Introduction

There are five species of true freshwater crabs of the family Potamidae on Okinawa Island, viz., *Geothelphusa levicervix* (Rathbun, 1898) sensu Minei (1973) (see Shokita *et al*. 2002: 446), *G. sakamotoana* (Rathbun, 1905), *G. tenuimanus* (Miyake and Minei, 1965) (for the ending of the specific name, see Naruse *et al*. 2004: 1218), *G. aramotoi* Minei, 1973, and *Candidiopotamon okinawense* Minei, 1973. *Geothelphusa tenuimanus* is endemic to Okinawa Island and is the most terrestrial of the Okinawan potamid crabs. Its distribution range can be roughly divided into northern and southern areas (Gima and Shokita 1980) (Fig. 1). Its habitat is associated with karst areas (Gima and Shokita 1980; Minei 1981; Shokita 1996a; Yoshigou 1999; habitat section below). Because of this, *G. tenuimanus* has been listed as a threatened species by Okinawa Prefecture and the Environment Agency (Environment Agency 1991; Okinawa Prefecture 1996).

Since the original description of *G. tenuimanus* there has been no taxonomic work on it except for the study of Yoshigou (1999), who pointed out morphological differences between the northern and southern populations but deferred a decision concerning their taxonomic significance. Because of the need for an effective conservation strategy for this species, it is important to understand the morphological diversity of its populations; furthermore, intraspecific morphological variation in freshwater decapods has rarely been discussed (but see Smith and Williams 1980;

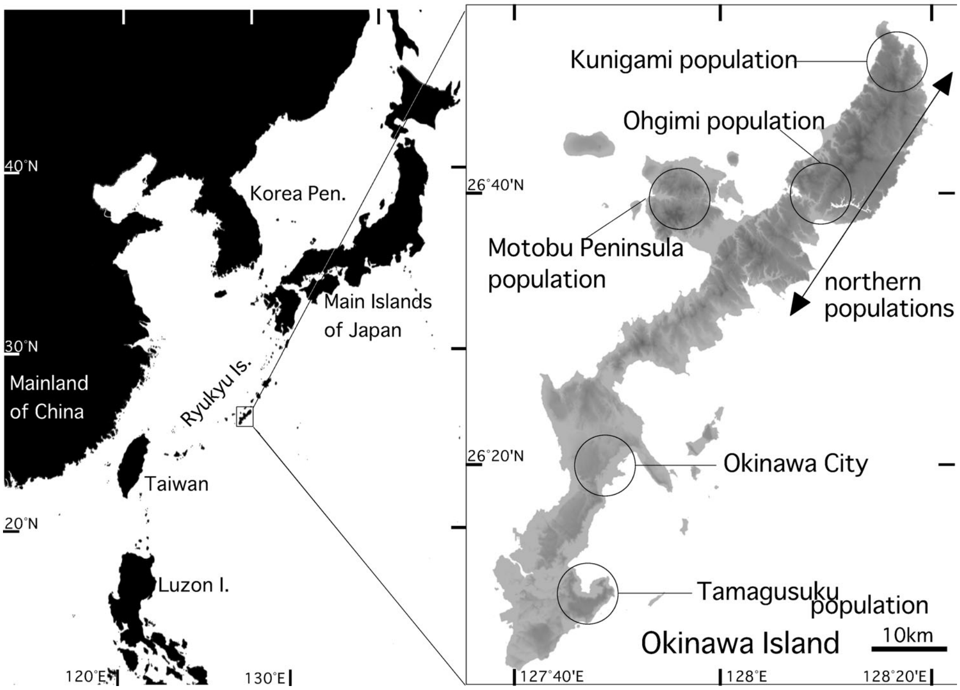

Fig. 1. Distribution of *Geothelphusa tenuimanus* on Okinawa Island.

Yeo *et al.* 1999). The present study aims to redescribe *G. tenuimanus* with consideration of its intraspecific variation.

Materials and Methods

The specimens used in this study have been deposited in the Natural History Museum and Institute, Chiba, Japan (CBM-ZC), the National Science Museum, Tokyo, Japan (NSMT), the Ryukyu University Museum, Fujukan, Okinawa, Japan (RUMF), and the Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan [specimens that have been transferred from the Zoological Laboratory, Kyushu University, Fukuoka, Japan (ZLKU)]. To increase the sample size of measurements, along with preserved specimens additional living individuals of the southern (=Tamagusuku) population were used. Foraging individuals of *Geothelphusa tenuimanus* were caught at night and brought back to the laboratory at the University of the Ryukyus. After measurement, crabs were released where they had been caught.

The terminology and measurements follow Ng (1988), Dai (1999), and Shy and Yu (1999). Carapace width level (indicating the distance between the middle of the posterior margin of the carapace and the point where the carapace width is greatest across the longitudinal median line) (Fig. 2) was also measured. Abbreviations are as follows: CL, carapace length; CW, carapace width; CWL, carapace width

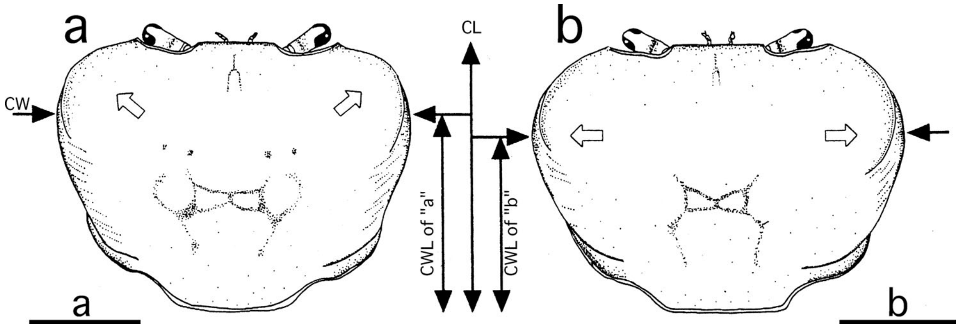

Fig. 2. Variation of carapace shape of *Geothelphusa tenuimanus*. a, Male (RUMF-ZC-47, CL 25.4 mm) collected from Kunigami population; b, male (RUMF-ZC-51, CL 23.5 mm) from Tamagusuku population. Open arrows indicate the direction of curvature of the anterolateral margins. Scales: 10 mm.

level; CH, carapace height; FW, frontal region width; EXW, width between external orbital angles; G1, male gonopod 1; G2, male gonopod 2.

Measurements of G1 and G2 to the nearest 0.01 mm were conducted using a stereomicroscope (Nikon SMZ-10) and a calibrated eyepiece micrometer. Other characters were measured to the nearest 0.1 mm using a digital slide caliper (Mitsutoyo CD-20C). For ratio values, a median value and a range (in parentheses) are provided. The CWL/CL ratio, the length/width ratio of the propodus and merus of the fourth ambulatory legs, and the shape of the G1 were compared in detail.

To reduce the effect on statistics of allometric growth associated with size, only preserved adult specimens were used for the ratio data in the species diagnosis below. In the present study, minimum adult size was provisionally defined for males by the smallest individual with the distal end of G1 exceeding the lower border of thoracic sternite 5, and for females by the smallest individual with the fifth abdominal segment equal to or wider than the third segment. Puberty sizes were thereby determined as 17.5 mm CL for males and 19.7 mm CL for females (Fig. 3).

Systematics

Genus ***Geothelphusa*** Stimpson, 1858
Geothelphusa tenuimanus (Miyake and Minei, 1965)
[Japanese name: Himeyuri-sawagani]
(Figs 2, 4, 7)

Potamon (*Geothelphusa*) *tenuimanus* Miyake and Minei, 1965: 377, pl. 21.
Geothelphusa levicervix Bott, 1970: 155 (in addendum). [*partim*]
Geothelphusa tenuimana: Minei 1968: 99, photogr. 13, 1973: 209, figs 5, 9A, B; Sakai 1976: 562 (English text), 347 (Japanese text); Gima and Shokita 1980: 9, 12, fig. 8; Minei 1981: 79, tables 2, 3, pl. 3 (upper); Miyake 1983: 152, 244, pl. 51 (6); Hirata *et al*. 1988: 11; Shokita 1990: 4, table 2; Environment Agency 1991: 220; Ng 1992: 160; Shy *et al*. 1994: 784; Okinawa Prefecture 1996: 362; Shokita 1996a: 464, pl.

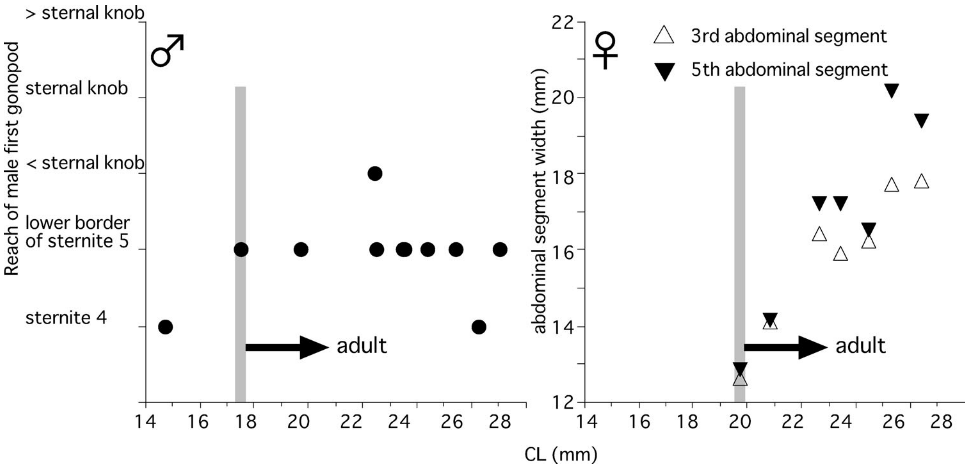

Fig. 3. Growth of relative length of male first gonopod and width of female third and fifth abdominal segments in *Geothelphusa tenuimanus*.

10, 1996b: 348, photogr. 1; Yoshigou 1999: 21, pl. 1 (I); Segawa 2000: 243, table 1, fig. 1; Shokita 2002: 167, pl 2; Kasai and Naruse 2003: 283, figs 67A, 68E.
Geothelphusa tenuimanus: Naruse *et al*. 2004: 1211.

Material examined (see Fig. 1). Kunigami population: 1 male, CL 24.4 mm, NSMT-Cr15114, coll. S. Shokita, T. Nagai, Y. Fujita, A. Kawakami, and H. Kawaguchi, 26 Dec. 1998; 1 male, CL 17.5 mm, RUMF-ZC-46 and 1 female, CL 26.4 mm, RUMF-ZC-45, coll. S. Shokita, T. Nagai, Y. Fujita, A. Kawakami, and H. Kawaguchi, 26 Dec. 1998; 1 male, CL 25.4 mm, RUMF-ZC-47 and 1 female, CL 24.4 mm, RUMF-ZC-48, coll. T. Naruse, 30 Jan. 2002.

Ohgimi population: 1 female, CL 19.7 mm, CBM-ZC 6588, coll. R. Segawa and N. Kochi, 7 Nov. 1997; 1 male, CL 22.5 mm, RUMF-ZC-11 and 1 female, CL 20.8 mm, RUMF-ZC-12, coll. T. Hayashi, 30 Sep. 1998; 1 female, CL 22.6 mm, RUMF-ZC-49, coll. S. Shokita, T. Nagai, Y. Fujita, A. Kawakami, and H. Kawaguchi, 27 Dec. 1998; 1 female, CL 25.3 mm, HMNH-C166, coll. H. Tamura, 1 Jun. 2000; 2 males, CL 19.7, 23.5 mm, HMNH-C167, 168, coll. H. Yoshigou, M. Iwao, and M. Iwasaki, 3 Jan. 2001.

Motobu Peninsula population: 1 male, CL 27.1 mm, ZLKU 9726 (holotype of *G. tenuimanus*), coll. S. Chinen, Aug. 1960; 1 male, CL 26.3 mm, RUMF-ZC-50, coll. S. Shokita, 1990.

Tamagusuku (=southern) population: 1 male, CL 22.4 mm, RUMF-ZC-10, coll. T. Sasaki and H. Tamura, 16 May 1998; 1 male, CL 23.5 mm, HMNH-C7, coll. H. Tamura, 25 May 1999; 1 male, CL 14.8 mm, HMNH-C164 and 1 female, CL 23.4 mm, HMNH-C165, coll. H. Yoshigou and N. Muraoka, 2 Jan. 2001; 1 male, CL 23.5 mm, RUMF-ZC-51, coll. T. Naruse, 21 May 2001.

Released individuals (Tamagusuku population): 3 males, CL 19.6–25.4 mm, coll. T. Naruse, 20 June 2003; 4 males, CL 20.74–23.4 mm, coll. T. Naruse, 21 June 2003.

Description. Carapace (Figs 2, 4a) ovate, dorsal surface flat and smooth, CW/CL ratio 1.35 (range 1.29–1.40), CW/CH ratio 2.49 (range 2.37–2.72), CL/CH ratio 1.85 (range 1.74–2.00); median groove shallow, postorbital and postfrontal cristae indistinct, gradually rising posteriorly; supraorbital margin not granulated, infraorbital margin granulated; external orbital angle obtuse, pointing anteriorly, FW/EXW ratio 0.39 (range 0.38–0.43), FW/CW ratio 0.23 (range 0.22–0.25); epibranchial tooth absent; anterolateral margin well demarcated, no cristae, no granules, with anterolaterally- to laterally-directed curvature; anterolateral and posterolateral regions smooth, subhepatic region swollen laterally; cervical groove very shallow, especially in small individuals; H-shaped gastric region distinct.

Eye (Fig. 4a) with developed cornea; subdistal part of cornea higher than peduncle in frontal view.

Mouthparts similar to those of *Geothelphusa miyakoensis* Shokita, Naruse, and Fujii, 2002 (*q.v.*), known from Miyako Island, southern Ryukyus, Japan, except for mandible (Fig. 4b) (inner-posterior margin of mandible sharp in *G. tenuimanus*) and third maxilliped (flagellum of exopod very short, just reaching inner margin of exopod in *G. tenuimanus*).

Chelae with distinct teeth along inner margin of both fingers, outer surface of manus smooth. Male chelae asymmetrical, male major chela (Fig. 4c) with inward-curving movable finger and ventrally-directed immovable finger, forming narrow gape when fingers closed. Cutting edge of immovable finger toothed, 2 large teeth present at 1/3 and 2/3 lengths, proximal one larger; movable finger with 2 large teeth, each tooth located slightly distal of corresponding large tooth of immovable finger. Female chelae slightly asymmetric in size.

Ambulatory legs very long, glabrous; propodi subovate in cross-sectional view, inner and outer sides each with 2 rows of small spines; dactyli also with row of spines on each of its 4 margins. Second ambulatory legs longest when stretched laterally, but almost same as third legs in length with 1.08 (range 1.02–1.21) length ratio, 2.97 (range 2.62–3.17) times as long as CL; length/width ratios of merus and propodus 6.10 (range 5.60–7.19) and 4.74 (range 4.25–5.02), respectively; propodus 0.91 (range 0.83–0.99) times as long as dactylus. Fourth ambulatory legs shortest, length/width ratios of propodus and merus 4.06 (range 3.53–4.82) and 5.40 (range 4.90–6.15), respectively.

Male abdomen triangular, length/width ratio 0.68 (range 0.61–0.79), tip of telson reaching imaginary line joining proximal 1/4 of cheliped coxae; distance from tip of telson to anterior margin of sternite 4 1.64 (range 1.32–1.97) times that to sternite 1–3; length/width ratio of male sixth abdominal segment 0.44 (range 0.41–0.48).

G1 (Fig. 4d) weekly sigmoid, with proximal half of subterminal segment and entire terminal segment directed inwards, and distal half of subterminal segment directed outwards, 3.00 (range 2.66–3.71) times as long as its width in total length measured from tip of G1 to basal end of median line on dorsal side; subterminal segment with tooth on outer proximal margin, but this tooth not developed in young individuals; terminal segment 2.09 (range 1.95–2.63) in length/width ratio, 0.16 (range 0.14–0.17) times as long as G1 total length; synovial membrane slightly bifurcate at distal margin, length/width ratio 3.25 (range 2.56–3.61). G2 with flagellum (Fig. 4e) short, 0.14 (range 0.12–0.18) times as long as G2 total length.

Remarks. *Shape of carapace* (Figs 2, 5, Tables 1, 2). The variation in the curvature of the anterolateral margin, represented by the CWL/CL ratio, was compared among the populations of *Geothelphusa tenuimanus*. For identically or similarly sized individuals, the Tamagusuku population tends to have a relatively lower

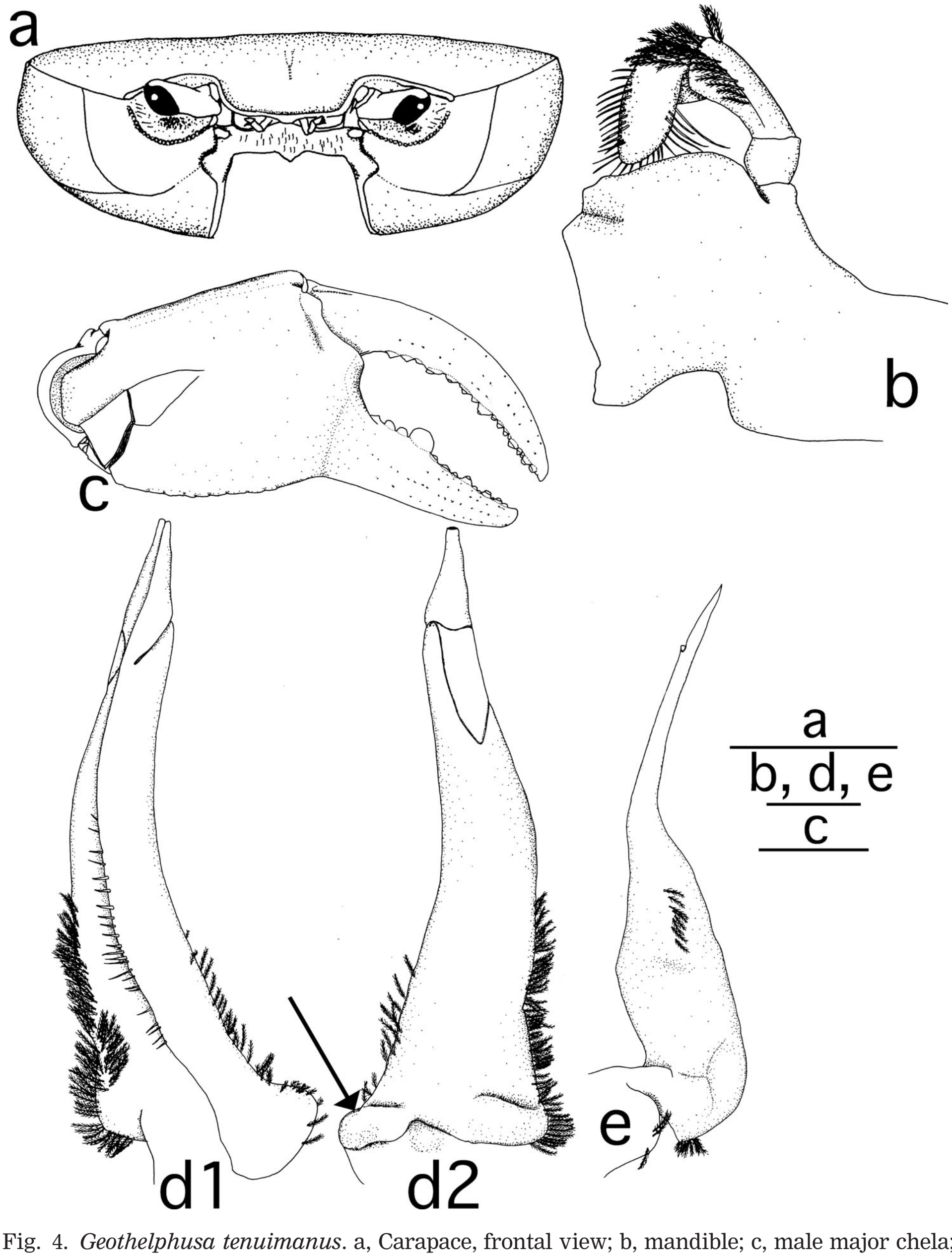

Fig. 4. *Geothelphusa tenuimanus*. a, Carapace, frontal view; b, mandible; c, male major chela; d1, ventral view of G1; d2, dorsal view of G1 (arrow indicates the outer posterial tooth); e, G2. a, b, RUMF-ZC-51, male CL 23.5 mm; c, ZLKU9726 (holotype), male, CL 27.1 mm; d, e, RUMF-ZC-47, male, CL 25.4 mm. Scales: 10 mm for a, c; 1 mm for b, d, e.

Table 1. Comparison of ratio characters among four populations of *Geothelphusa tenuimanus*.

Populations	CWL/CL	Propodus length/ width in 4th ambulatory leg	Merus length/ width in 4th ambulatory leg
Kunigami	0.73 (0.72–0.76)	3.94 (3.67–4.32)	5.34 (4.90–5.77)
Ohgimi	0.75 (0.70–0.81)	4.23 (4.01–4.70)	5.43 (5.26–5.68)
Motobu Peninsula	0.67 (0.67–0.67)	4.44 (4.07–4.82)	5.67 (5.19–6.15)
Pooled northern	0.73 (0.67–0.81)	4.22 (3.67–4.82)	5.40 (4.90–6.15)
Tamagusuku	0.68 (0.65–0.72)	3.74 (3.34–4.04)	5.09 (4.44–5.47)

Median value and range (in parentheses) of the ratio values are provided for each character. Kunigami, Ohgimi, and Motobu populations are *a priori* pooled as the northern population.

Table 2. Comparisons of measurements of carapace and fourth ambulatory legs among populations of *Geothelphusa tenuimanus*.

Characters	*SS*	*df*	*MS*	*F*	*P*	Multiple comparison
CWL	1.589	3	0.530	2.111	0.133	K^a O^a M^a T^a
	0.294	1	0.294	0.602	0.446	N^b T^b
Propodus L	3.343	3	1.114	22.822	<0.001	
	0.256	1	0.256	1.096	0.306	N^c T^c
Propodus W	0.139	3	0.046	2.292	0.111	K^d O^d M^d T^d
	0.001	1	0.001	0.022	0.883	N^e T^e
Merus L	6.283	3	2.094	23.999	<0.001	
	0.295	1	0.295	0.723	0.404	N^f T^f
Merus W	0.343	3	0.114	3.210	0.046	
	0.042	1	0.042	0.811	0.377	N^g T^g

The characters were compared by ANCOVA with Bonferroni test using CL as the covariate. Upper and lower lines show the comparisons among 4 populations and between pooled northern and southern populations, respectively. Kunigami, Ohgimi, and Motobu populations are *a priori* pooled as the northern population. Taxa sharing the same superscript letter showed no significant difference in the Bonferroni test.
Abbreviations: *df*, degrees of freedom; *F*, *F* statistic; K, Kunigami population; L, length; M, Motobu Population; *MS*, mean squares; N, pooled northern population; O, Ohgimi population; *P*, probability; *SS*, sum of squares; T, Tamagusuku (=southern) population; W, width.

CWL than the northern one. Larger individuals tend to have a lower CWL than smaller one in both the Tamagusuku and northern populations (Fig. 5, Table 1). However, there are no significant differences in ANCOVAs tested among all the populations or between pooled northern and southern populations (Table 2).

Length/width ratio of propodus of fourth ambulatory leg (Fig. 6a, b, Tables 1, 2). The Tamagusuku population tends to have a lower length/width ratio of the propodus of this leg article. On the other hand, the Ohgimi population has a relatively large value while the Kunigami population has an intermediate one. The regression lines between CL and propodus length of the fourth ambulatory leg show that the Tamagusuku population has a relatively shorter propodus than the pooled northern populations (Fig. 6a, b, Table 1). However, there are no significant differences in ANCOVAs in either propodus length or width (Table 2).

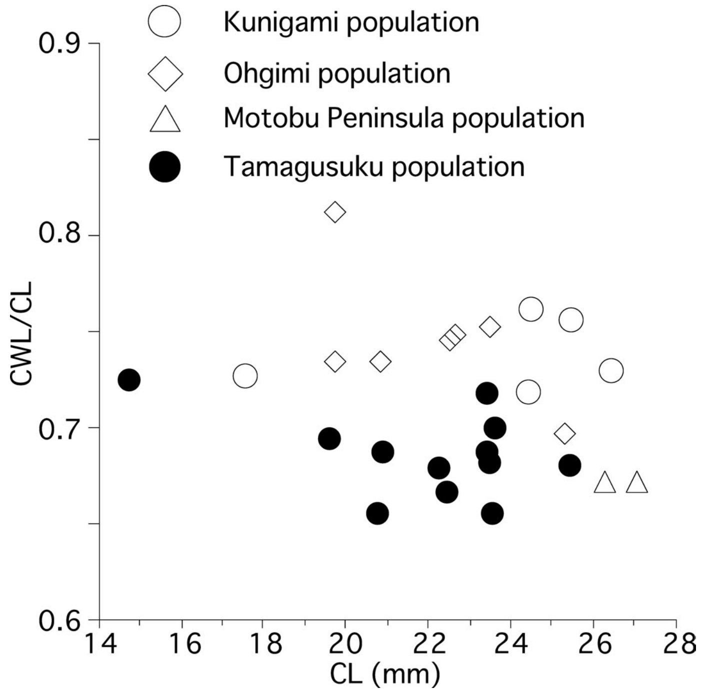

Fig. 5. Comparison of curvature of anterolateral margin of carapace among Okinawa Island populations of *Geothelphusa tenuimanus*. The curvature of the anterolateral margin of the carapace is represented by the CWL/CL ratio. Open symbols, northern populations; closed symbol, southern (Tamagusuku) population.

Length/width ratio of merus of fourth ambulatory leg (Fig. 6c, d, Tables 1, 2). The merus shows a similar tendency as the propodus concerning the length/width ratio, but the Tamagusuku and northern pooled populations are less differentiated. ANCOVAs also shows no significant differences in either merus length or width (Table 2).

G1 (Fig. 4d). The tooth on the outer proximal margin of the basal segment is slightly variable in size, but it is always present in large individuals.

Color variation (Fig. 7). Coloration of the carapace and ambulatory legs is variable individually from purple to brown.

Habitat. *Geothelphusa tenuimanus* occurs patchily on montane to submontane karstic areas of Okinawa Island. The crabs are also present inside limestone caves in these areas. The epigeal individuals hide under limestone rocks in the day and come out at night. They seem to prefer barely moistened soil and rarely dig burrows by themselves, except during the rainy period when the soil is wet. Hypogeal individuals were observed to climb on stalactites in a cave in Ohgimi Village (H. Yoshigou and H. Tamura, pers. comm.).

Miyake and Minei (1965: 381) stated that "*G. tenuimanus* dwells at the upper reaches of rivers, and they are hiding under rocks or burrows at the wet place of riversides." This observation differs from ours.

Distribution. Okinawa Island, Central Ryukyus, Japan.

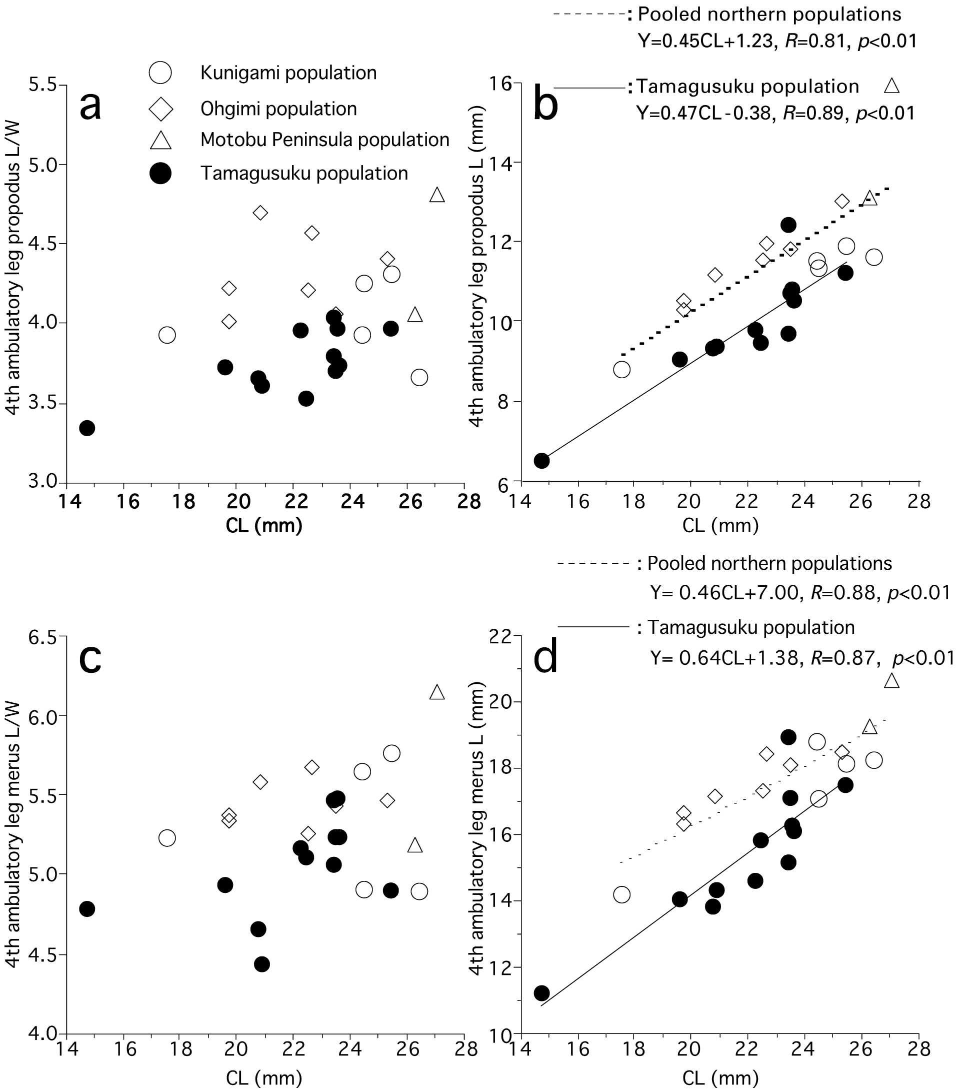

Fig. 6. Comparison of allometric growth of propodus and merus of fourth ambulatory leg among Okinawa Island populations of *Geothelphusa tenuimanus*. a, Length/width ratio of propodus; b, regression of propodus length on carapace length; c, length/width ratio of merus; d, regression of merus length on carapace length. Kunigami, Ohgimi, and Motobu populations were *a priori* pooled as the northern population. Open symbols, northern population; closed symbol, southern (Tamagusuku) population.

Discussion

Yoshigou (1999) stated that populations in the north of Okinawa have a length/width ratio of 6 for the fourth ambulatory propodus but that those from the south only have a ratio of 4. We have examined a large series of specimens from

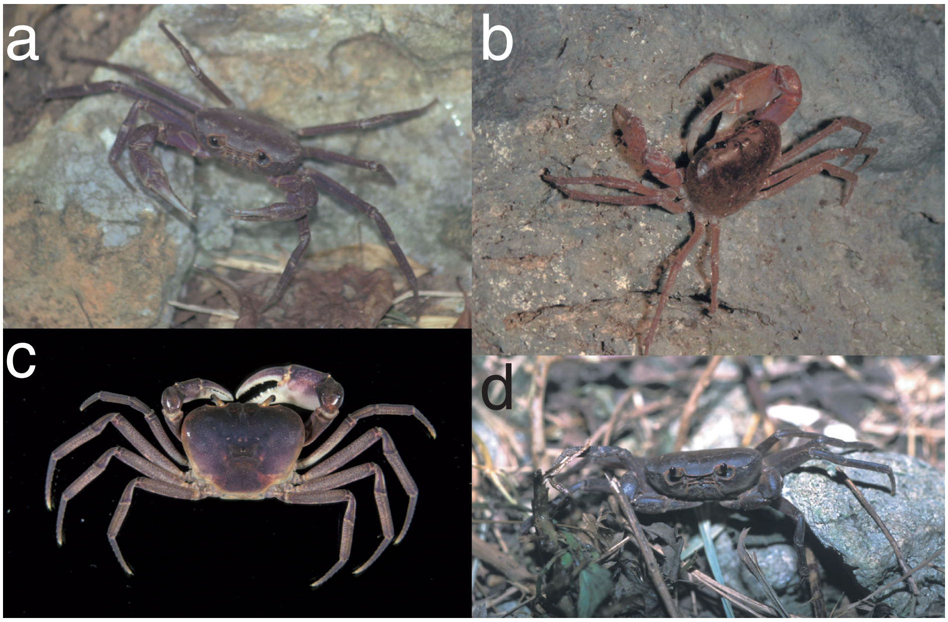

Fig. 7. Color variation of *Geothelphusa tenuimanus*. a, An indivisual from Kunigami population; b, from Okinawa City, c, d, from Tamagusuku population. Photographs by S. Shokita (a), Y. Chigira (b), and T. Naruse (c, d).

both northern and southern Okinawa, as well as those used by Yoshigou (1999), and the length/width ratios we found for the ambulatory propodus in the northern and Tamagusuku populations are only 4.22 (range 3.67–4.82) and 3.74 (range 3.34–4.04), respectively. Yoshigou (1999) stated he had measured the propodus, but he probably did so incorrectly (see Table 1). As Yoshigou (1999) has pointed out, the Tamagusuku population also tends to have more laterally-directed anterolateral margins of the carapace and a shorter propodus length of the fourth ambulatory legs. However, these variations are not very significant and there is no difference in the appearance of the taxonomically important G1; therefore, the four compared populations are here regarded as conspecific. On the other hand, from the point of view of conservation, the presence of morphological disparity among the populations should be emphasized.

The present material comes only from the northern and southern parts of the island of Okinawa; however, there are other areas, also in the central part of the island, that have exposed limestone (see Kizaki 1985, fig. III B-1-1). Many of the limestone areas in the island's center have been severely disturbed, and pristine habitats are scarce. Because potamid crabs do not have marine pelagic larval phases, they may be easily isolated by disconnection of adult habitats. Hidenori Chigira (pers. comm.) recently photographed a specimen (Fig. 7b) clearly referable to *Geothelphusa tenuimanus* from Okinawa City in the center of the island. This is an area we have yet to explore in depth, but this finding suggests that *G. tenuimanus* has a wider distribution than just the less disturbed northern and southern parts of Okinawa. Certainly, this could explain why there are only minor morphological differences between these populations.

Recently fossils of *G. tenuimanus* were collected in the southern part of Okinawa Island from clay within a fissure in limestone of the Middle Pleistocene Ryukyu Group (Naruse *et al*. 2004). Naruse *et al*. (2004) estimated the geological age of the fossil *G. tenuimanus* as the Late Pleistocene. Kizaki and Oshiro (1977) hypothesized that, in the Late Pleistocene, land areas expanded to form several super-islands, Okinawa Island having then been continuous with the Kerama Group and Kume Island (Kizaki and Oshiro 1977, fig. 11). This hypothesis has been advocated by several authors with minor modification (e.g., Kizaki and Oshiro 1980; Ota 1998). It is therefore puzzling that *G. tenuimanus* appears to be absent on these islands today.

Geothelphusa tenuimanus has been observed inside limestone caves (see habitat section above). Cavernicolous crabs often show morphological adaptations for a hypogeal lifestyle. Rodriguez (1985) listed the characteristics of cave-adapted crabs as follows: (1) long and slender legs; (2) depigmentation of the legs and carapace; (3) translucence; and (4) a reducted and/or poorly developed cornea. Guinot (1988) focused on the ocular morphology, the troglobytic crabs being categorized into three types: (1) those with partially reduced eyes together with an eyestalk that tapers in its distal extreme and, accordingly, has a reduced cornea; (2) those with the eyes reduced overall, with the peduncle very short and more or less stuck in the orbit, without any trace of cornea and peduncle; and (3) those not with reduced eyes but with a stuck peduncle, without cornea and pigments. However, many cave-occurring brachyurans, including *G. tenuimanus*, possess few such cave-adapted characters. For example, *Stygothelphusa bidiensis* (Lanchester, 1900) (Gecarcinucidae) has long and slender legs but fully developed eyes; it is not a complete troglobite and does not appear to be entirely confined to the twilight zones of caves (Ng 1989). Ng (1989) speculated that *S. bidiensis* is an amphibious species, the long legs being advantageous in the soft substrate covered by guano and mud. Near-shore cave dwellers, such as *Discoplax longipes* A. Milne Edwards, 1867 and *D. gracilipes* Ng and Guinot, 2001 (Gecarcinidae), also have elongated legs but well developed eyes. Ng and Guinot (2001) stated that young individuals of these species like to stay in water but adults wander on the forest floor or over limestone structures, sometime far from water. *Geothelphusa tenuimanus* has elongated and slender legs, as well as well developed eyes, but the extent to which it depends on caves is unknown. It is noteworthy that even juveniles of this species (e.g., 10.8 mm CL) have been observed in limestone-associated epigeal habitats together with adults (Shokita, unpublished data). It seems that *G. tenuimanus* is more terrestrial than *Stygothelphusa bidiensis* and *Discoplax* species, preferring drier soils that are not waterlogged (Gima and Shokita 1980), at least in epigeal habitats. Simultaneously, the presence of the juveniles in epigeal habitats implies that the main habitat of *G. tenuimanus* is epigeal.

Socotra pseudocardisoma Cumberlidge and Wranik, 2002 (Potamidae), from Socotra Island, Yemen, has much in common with *Geothelphusa tenuimanus* with regard to habitat, dwelling in the crevices of surface limestone. The type locality was described as "a part of the island where limestone is dominant, and where climatic erosion of the calcareous substratum has produced sinks, underground streams, caverns, hollows and crevices", and *S. pseudocardisoma* was observed wandering on the surface at night (Cumberlidge and Wranik 2002).

Geothelphusa tenuimanus possesses distinctly longer and more slender ambulatory legs and a flatter carapace than its congeners; however, its diagnostic characters, such as the general shape of the carapace and G1, are shared with members of *Geothelphusa* (see Shy *et al*. 1994). Segawa (2000), in a molecular study of the phylogeny of Japanese potamid crabs, suggested that *G. tenuimanus* forms a monophyletic group with *G. levicervix* sensu Minei (1973), *G. miyakoensis*, and *G.* sp. from Tokashiki Island, and that this group is the sister group of *G. aramotoi*. If this is correct, then *G. tenuimanus* is not a generically distinct entity. The unusual appearance of *G. tenuimanus* is probably an adaptation for the karst environment and a facultatively cavernicolous lifestyle.

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References

Bott, R. 1970. Die Süßwasserkrabben von Europa, Asien, Australien und ihre Stammesgeschichte. Eine Revision der Potamoidea und der Parathelphusoidea. (Crustacea, Decapoda). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 526: 1–338.

Cumberlidge, N. and Wranik, W. 2002. A new genus and new species of freshwater crab (Potamoidea, Potamidae) from Socotra Island, Yemen. Journal of Natural History 36: 51–64.

Dai, A.-Y. 1999. *Fauna Sinica Arthropoda Crustacea Malacostraca Decapoda Parathelphusidae Potamidae*. Science Press, Beijing, xiii+501 pp., 1 colour pl., 30 pls. [In Chinese with English abstract]

Environment Agency 1991. Brackish and freshwater decapod crustaceans. Pp. 211–230. *In*: Environment Agency (Ed.) *Threatened Wildlife in Japan: Red Data Book on Invertebrates*. Japan Wildlife Research Center, Tokyo. [In Japanese]

Gima, H. and Shokita, S. 1980. Distribution of potamonid crabs in the Yona River of Okinawa Island, the Ryukyus. Biological Magazine, Okinawa 18: 9–15. [In Japanese with English abstract]

Guinot, D. 1988. Les crabes cavernicoles du monde. Mémoires de Biospéologie 15: 3–40.

Hirata, Y., Nakasone, Y. and Shokita, S. 1988. *Okinawan Decapods and Shells in Color*. Fudokisha Publishing, Naha, 144 pp. [In Japanese]

Kasai, H. and Naruse, T. 2003. Potamidae. Pp. 282–288. *In*: Nishida, M., Shikatani, N. and Shokita, S. (Eds) *The Flora and Fauna of Inland Waters in the Ryukyu Islands*. Tokai University Press, Tokyo. [In Japanese]

Kizaki, K. 1985. *Geological Studies of the Ryukyu Arc*. Okinawa Times, Naha, 278 pp. [In Japanese]

Kizaki, K. and Oshiro, I. 1977. Palaeogeography of the Rytkyu [*sic*] Islands. Marine Science Monthly 9: 542–549. [In Japanese with English abstract]

Kizaki, K. and Oshiro, I. 1980. The origin of the Ryukyu Islands. Pp. 8–37. *In*: Kizaki, K. (Ed.) *Natural History of the Ryukyus*. Tsukiji-shokan, Tokyo. [In Japanese]

Minei, H. 1968. [Fresh-water crabs of Japan]. Nature Study 14: 94–99. [In Japanese]

Minei, H. 1973. Potamoid crabs of the Ryukyu Islands, with descriptions of five new species (Crustacea, Decapoda, Potamoidea). Journal of the Faculty of Agriculture, Kyushu University 17: 203–226.

Minei, H. 1981. Distribution and general habitat of the freshwater crabs of Japan. Pp. 79–92. *In*: Yamaguchi, T. (Ed.) *Ecological Studies of Coastal Marine and Freshwater Crabs. (Report for the Grant-in-Aid for Co-operative Research, 1978–1980, A, No. 334035)*. Ministry of Education, Tokyo. [In Japanese]

Miyake, S. 1983. *Japanese Crustacean Decapods and Stomatopods in Color. Vol. II Brachyura (Crabs)*. Hoikusha, Osaka, iii+277 pp., 64 pls. [In Japanese]

Miyake, S. and Minei, H. 1965. A new fresh-water crab, *Potamon* (*Geothelphusa*) *tenuimanus* sp. nov. from Okinawa-jima, the Ryukyu Islands. Science Bulletin of the Faculty of Agriculture, Kyushu University 21: 377–382, pl. 21. [In Japanese with English Summary]

Naruse, T., Karasawa, H., Shokita, S., Tanaka, T. and Moriguchi, M. 2004. A first fossil record of the terrestrial crab, *Geothelphusa tenuimanus* (Miyake & Minei, 1965) (Decapoda, Brachyura, Potamidae) from Okinawa Island, Central Ryukyus, Japan. Crustaceana 76 [for 2003]: 1211–1218.

Ng, P. K. L. 1988. *The Freshwater Crabs of Peninsular Malaysia and Singapore*. Shinglee Press, Singapore, viii+156 pp., 4 colour pls.

Ng, P. K. L. 1989. The identity of the cavernicolous freshwater crab *Potamon* (*Thelphusa*) *bidiense* Lanchester, 1900 (Crustacea: Decapoda: Brachyura: Gecarcinucidae) from Sarawak, Borneo, with description of a new genus. The Raffles Bulletin of Zoology 37: 63–72.

Ng, P. K. L. 1992. A new genus and species of cavernicolous crab (Brachyura: Potamidae) from Kanchanaburi, Thailand, with comments on the genera *Tiwaripotamon* Bott, 1970 and *Larnaudia* Bott, 1966. Mémoires de Biospéologie 19: 159–167.

Ng, P. K. L. and Guinot, D. 2001. On the land crabs of the genus *Discoplax* A. Milne Edwards, 1867 (Crustacea: Decapoda: Brachyura: Gecarcinidae), with description of a new cavernicolous species from the Philippines. The Raffles Bulletin of Zoology 49: 311–338.

Okinawa Prefecture 1996. Crustaceans. Pp. 362–385. *In*: Nature Conservation Division (Department of Environment and Health, Okinawa Prefectural Government) (Ed.) *Red Data Okinawa*. Nature Conservation Division, Department of Environment and Health, Okinawa Prefectural Government, Naha. [In Japanese]

Ota, H. 1998. Geographic patterns of endemism and speciation in amphibians and reptiles of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. Research on Population Ecology 40: 189–204.

Rodriguez, G. 1985. A new cavernicolous crab (Crustacea, Decapoda, Pseudothelphusidae) from Colombia. Bioloski Vestnik 2: 73–80.

Sakai, T. 1976. *Crabs of Japan and the Adjacent Seas*. Kodansha, Tokyo, xxix+773 pp. [English text]+461 pp. [Japanese text]+251 pp. [plate volume].

Segawa, R. 2000. Molecular phylogenetic study of potamoid crabs in Ryukyu Islands. Kaiyo Monthly 32: 241–245. [In Japanese]

Shokita, S. 1990. Inland-water macrofauna and their fluctuations in the northern part of Okinawa Island, the Ryukyus. Biological Magazine, Okinawa 27: 3–13. [In Japanese with English abstract and captions]

Shokita, S. 1996a. *Geothelphusa tenuimana*. Pp. 464–466, pl. 10. *In*: Japan Fisheries Resource Conservation Association (Ed.) *Basic Information on Rare Wild Aquatic Animals in Japan (III)*. Japan Fisheries Resource Conservation Association, Tokyo. [In Japanese]

Shokita, S. 1996b. The origin of land-locked freshwater shrimps and potamoids from the Ryukyu Islands, southern Japan. Journal of Geography 105: 343–353. [In Japanese with English abstract and captions]

Shokita, S. 2002. The origin of the terrestrial and freshwater crustacean fauna of the Ryukyu Islands, southern Japan. Pp. 163–173. *In*: Kimura, M. (Ed.) *The Formation of the Ryukyu Arc and Migration of Biota to the Arc*. Okinawa Times, Naha.

Shokita, S., Naruse, T. and Fujii, H. 2002. *Geothelphusa miyakoensis*, a new species of freshwater crab (Crustacea: Decapoda: Brachyura: Potamidae) from Miyako Island, Southern Ryukyus, Japan. The Raffles Bulletin of Zoology 50: 443–448.

Shy, J.-Y. and Yu, H.-P. 1999. *Freshwater Crabs of Taiwan*. National Museum of Marine Biology and Aquarium, Pingtung, IV+ii+116 pp. [In Chinese]

Shy, J.-Y., Yu, H.-P. and Ng, P. K. L. 1994. Crabs of the genus *Geothelphusa* Stimpson, 1858 (Crustacea: Decapoda: Brachyura: Potamidae) from Taiwan, with descriptions of 25 new species. The Raffles Bulletin of Zoolology 42: 781–846.

Smith, M. J. and Williams, W. D. 1980. Infraspecific variation within the Atyidae: a study of morphological variation within a population of *Paratya australiensis* (Crustacea: Decapoda). Australian Journal of Marine and Freshwater Research 31: 397–407.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum quae in Expeditions ad Oceanum Pacificum Septentrionalem a Republica Federate missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars V. Crustacea Ocypodoidea. Proceedings of the Academy of Natural Sciences of Philadelphia 10: 93–110.

Yeo, D. C. J., Cai, Y. and Ng, P. K. L. 1999. The freshwater and terrestrial decapod Crustacea of Pulau Tioman, Peninsular Malaysia. The Raffles Bulletin of Zoology, Supplement 6: 197–244.

Yoshigou, H. 1999. Potamidae (Crustacea: Decapoda: Brachyura) of Japan. Hibakagaku: Journal of the Hiba Society of Natural History (191): 17–26, pls I, II. [In Japanese]