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Morphological and Molecular Evidence Revealed the Taiwanese Hydrothermal Vent Crab *Xenograpsus testudinatus* NK Ng, Huang & Ho, 2000 is a Junior Synonym of *X. novaeinsularis* Takeda & Kurata, 1977 in Japan (Crustacea: Brachyura: Thoracotremata: Xenograpsidae)

Hironori Komatsu[1], Chien-Hui Yang[2,*], Tin-Yam Chan[2], and Peter K.L. Ng[3]

[1]*Department of Zoology, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan. E-mail: h-komatu@kahaku.go.jp (Komatsu)*

[2]*Institute of Marine Biology and Center of Excellence for the Oceans, National Taiwan Ocean University, Keelung 202301, Taiwan. *Correspondence: E-mail: chyang@ntou.edu.tw (Yang) E-mail: tychan@ntou.edu.tw (Chan)*

[3]*Lee Kong Chian Natural History Museum (LKCNHM), 2 Conservatory Drive, Singapore 117377, Singapore. E-mail: peterng@nus.edu.sg (nG)*

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Hironori Komatsu: https://orcid.org/0000-0002-7573-4127
Chien-Hui Yang: https://orcid.org/0000-0002-4594-3622
Tin-Yam Chan: https://orcid.org/0000-0002-8143-0007
Peter K. L. Ng: https://orcid.org/0000-0001-5946-0608

The hydrothermal vent crab *Xenograpsus testudinatus* NK Ng, Huang & Ho, 2000 (Xenograpsidae), originally described from Kueishan in northern Taiwan, has the been the subject of many ecological and physiological studies in the island and Japan. The species is morphologically similar to the Japanese *X. novaeinsularis* Takeda & Kurata, 1977, reported from Ogasawara Islands, being supposedly separated by characters of the carapace, proportions and form of the third maxillipeds, chelae, ambulatory legs male pleon and male first gonopod. Earlier studies have shown that most of these differences are not taxonomically reliable and only some carapace characters are able to distinguish them. Genetic analyses of the mitochondrial *COI* and 16S rRNA genes from specimens of both species across the distribution, including material from or adjacent to their type localities, confirm that previous diagnostic interspecific characters are intraspecific variations, and even the carapace differences do not work. *Xenograpsus testudinatus* is here regarded as a junior synonym to *X. novaeinsularis*. *Xenograpsus* currently contains two species, with *X. novaeinsularis* in the West Pacific and *X. ngtama* McLay, 2007, from New Zealand, with the two species being morphologically and genetically distinct.

Keywords: Integrated taxonomy, Distribution, Type material, Synonymy, Hydrothermal vent crab

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BACKGROUND

The genus *Xenograpsus* Takeda & Kurata, 1977 contains two species in the West Pacific and one species in New Zealand. *X. novaeinsularis* Takeda & Kurata, 1977, was originally described from three specimens (two males and one female) collected from shallow water volcanic vents at Nishinoshima island, Ogasawara Islands, a volcanic island created in 1973 in Japan (Kido and Koike 1975; Murano 1975; Nakamura and Koike 1975; Yamazi and Wakamiya 1975). *Xenograpsus testudinatus* NK Ng, Huang & Ho, 2000, was described from 12 males and 11 females from shallow volcanic vents at Kueishan (= Turtle Mountain) Island, Ilan County, and an adjacent fishing port in Taiwan (NK Ng et al. 2000). McLay described a third species, *X. ngatama*, from New Zealand (McLay 2007). On the basis of a suite of morphological and genetic characters, NK Ng et al. established a new family, Xenograpsidae, for the genus (NK Ng et al. 2007), and this has been supported in subsequent molecular studies (*e.g.*, Schubart and Cuesta 2010; Tsang et al. 2022).

The Taiwanese species, *X. testudinatus*, has been the subject of many studies, including ecology, development, genetics and general biology; especially around the shallow water vent systems in Kueishan Island (e.g., Jeng et al. 2004a, b; Wang et al. 2013, 2014; Chan et al. 2016; Yang et al. 2016; Allen et al. 2020; Yang et al. 2022; Chen et al. 2025) (see review by Thirunavukkarasu et al. 2025); and the species has also been reported from southern Japan (NK Ng et al. 2014). However, there has been some doubt if *X. testudinatus* is a separate species from *X. novaeinsularis*, and NK Ng et al. (2014) observed that almost all the morphological characters that have been used to discriminate them do not work. Previous genetic studies also done, especially on the Taiwanese and southern Japanese material of *X. testudinatus* by NK Ng et al. 2014 and Yang et al. 2022. NK Ng et al. (2014: 397) commented that "The low variation of divergence and even the identical haplotypes shared between the Taiwanese and Japanese COI strongly suggests that there is good gene flow between the two localities, probably via the connected Okinawa Trough." with Yang et al. (2022: 11) adding,

"that it *X. testudinatus* has a relatively slow molecular differentiation rate with low genetic divergences across depth and geography, may be associated with its highly specialized habitat requirements …..The strong dispersal of *X. testudinatus* in the West Pacific also casts doubt on its taxonomic validity, where it is likely to be conspecific with the Japanese vent crab *X. novaeinsularis* ….. *Xenograpsus novaeinsularis* and *X. testudinatus* are morphologically very close and there is enough variation to suggest they may be the same.".

Unfortunately, no genetic sequences are available for *X. novaeinsularis*, with NK Ng et al. (2014) noting that they could not obtain sequences from the tissues of the type specimens or from the material reported by Türkay & Sakai (1995) from the Marianas. Oda et al. (2022) discussed dispersion of larvae along the Kuroshio for *Xenograpsus* but as they did not have genetic data of *X. novaeinsularis* from the type locality, provisionally identified their material to *X. testudinatus*; although their discussion and datasets suggested the two taxa were conspecific (Oda et al. 2022).

The present study based on an integrative approach, to re-examine all the morphological and genetic characters that have been used to diagnose *X. testudinatus* from *X. novaeinsularis*, using material from Taiwan and Japan, as well as comparative material of *X. ngatama*. This includes recently obtained the partial sequences of mitochondrial genes (COI and 16S rRNA) from fresh material collected from near the type locality of *X. novaeinsularis*.

MATERIALS AND METHODS

Sample collections

Specimens examined are deposited in the National Museum of Nature and Science (NSMT), Tsukuba, Japan; Crustacean Collection of the Taiwan National Museum (TMCD), Taipei, Taiwan; Zoological Collection of Biodiversity Research Museum, Academia Sinica (ASIZ), Nankang, Taiwan; National Taiwan Ocean University (NTOU), Keelung, Taiwan; Senckenberg Research Institute and Natural History Museum (SMF), Frankfurt, Germany; National Institute of Water and Atmosphere Invertebrate Collection (NIWA), Wellington, New Zealand; and Zoological Reference Collection (ZRC), Lee Kong Chian Natural History Museum, National University of Singapore.

Morphological analysis

For the morphological work, measurements provided, in millimetres, are of the maximum carapace width and length, respectively. The terminology used follows Davie et al. (2015). The

synonymies for the species are restricted to publications that discuss the taxonomy. The abbreviations G1 and G2 are used for the male first and second gonopods, respectively.

NK Ng et al. (2007) had separated *X. testudinatus* from *X. novaeinsularis* by 11 characters: armature on the anterolateral margin of the carapace, relatively prominence of the epigastric cristae, relative convexity of the dorsal surface of the carapace, degree of development of the anteroexternal margin of the third maxilliped merus, relative proportions of the merus of the cheliped, proportions of the ambulatory propodus and dactylus, shape of the ambulatory merus, and structures of the male telson and G1. NK Ng et al. (2014) had reappraised all the characters at length after comparing the types as well as material from Taiwan and southern Japan, concluded that all except one of the differences can be explained by variation. Even the G1 structures, typically diagnostic for species, were determined to be not useful. They observed that the only character that appeared to work was whether the anterolateral margin was armed – with an epibranchial tooth in *X. testudinatus* or with the margin entire and without trace of a tooth in *X. novaeinsularis*. NK Ng et al. (2014) noted, however, that they did not have a good series from central Japan and the type locality, and preferred to keep the two species separate until more Japanese material became available. This shortcoming is now resolved in the present study and allows the sole diagnostic character of the absence/presence of an epibranchial tooth to be tested.

Molecular analysis

We also obtained the molecular dataset for three males and one female from Kita-Iwo-to Island, Ogasawara Archipelago (NSMT) as well as two males and a female from the Izu Islands (NSMT). Crude genomic DNA of these seven individuals were extracted from the cheliped muscles using the QIAGEN® DNeasy Blood and Tissue Kit (69504, Valencia, CA, USA) following the protocol of the manufacturer. Primer sets, chemicals composition for reaction, cycling profiles, product checking and sequencing procedures of PCR followed those used in Yang et al. (2022). Additional sequences were downloaded from the GenBank (viz. NK Ng et al. 2014; Miyake et al. 2019; Oda et al. 2022; Yang et al. 2022) and added with the new sequences in this study for a comparison. There are 222 and 153 sequences of mitochondrial COI and 16S rRNA genes respectively from the GenBank including *X. ngatama* (KY985236) as the outgroup (Table 1). A total of 229 COI sequences (491–657 bp) were separated into six populations for the analyses, including the deep-sea (TD) and shallow waters (TS) of Kueishan Island in Taiwan, Kita-Iwo-to Island (J_Ki), Showa Iojima (J_Sho), Shikine-jima (J_Shi) and Omuro-dashi (J_Omu) in Japan (e.g. Miyake et al. 2019; Oda et al.

2022; Yang et al. 2022). The dataset of 16S rRNA gene (427–545 bp) includes 160 sequences and separated into five populations except Omuro-dashi (Tables 1–3). The missing nucleotides within the dataset were replaced by the fifth nucleotide "N" for performing the subsequent analyses. Sequence alignment was performed by MAFFT v.7 online service (Katoh et al. 2019) and corrected pairwise distance was calculated based on Kimura 2-parameters (K2P) model (Kimura 1980) by MEGA v. 11 (Tamura et al. 2021). DnaSP v.6.12.03 (Rozas et al. 2017) was used to calculate the numbers of haplotype then converted to the analytic format. Arlequin v.3.5 (Excoffier and Lischer 2010) was used to estimate the F_{ST} value for evaluating the genetic differentiation between each population and 1000 permutations were implemented to assess the significance of the statistics. Network v. 10.2.0.0. (https://www.fluxus-engineering.com/network terms.htm, accessed on 30 Dec. 2020) was used to construct the haplotype networks by using the median-joining algorithm for examining the genealogy of the haplotypes on these *Xenograpsus* populations.

Table 1. Samples and sequences of *Xenograpsus* Takeda & Kurata, 1977 used in this study. "*" Numbers of haplotype

Species (Defined in the studies)	Sampling locality [population abbreviation]	Sample size	Accession Numbers	Reference
X. novaeinsularis	Kita-Iwo-to Island, Ogasawara, Japan [J_Ki]	4	COI (XXXXXXXX–XXXXXXXX) 16S (XXXXXXXX–XXXXXXXX)	This study
	Omura-dashi, Izu Island, Japan [J_Omu]	3	COI (XXXXXXXX–XXXXXXXX) 16S (XXXXXXXX–XXXXXXXX)	
X. testudinatus	Kueishan Island (shallow water), Ilan, Taiwan [TS]	1	COI (EU727203)	Ki et al. 2009
		4	COI (AB933570–AB933573)	Ng et al. 2014
		50	COI (OM764349–OM764360, OM764362–OM764399,) 16S (OM777525–OM777575)	Yang et al. 2022
	Kueishan Island (deep sea), Ilan, Taiwan [TD]	70	COI (OM764400–OM764469) 16S (OM777576–OM777645)	Yang et al. 2022
	Showa Jima, Kagoshima, Japan [J_Sho]	5	COI (AB933569, AB933574–AB933577)	Ng et al. 2014
		30	COI (OM764470–OM764499) 16S (OM777646–OM777675)	Yang et al. 2022
		26	COI (OK017074–OK017076, OK017082, OK017084–OK017088)*	Oda et al. 2022
	Shikine Jima, Izu, Japan [J_Shi]	3	COI (LC490686–LC490688)	Miyake et al. 2019
		8	COI (OK017074, OK017075, OK017088, OK017090)*	Oda et al. 2022
	Omuro-dashi, Izu, Japan [J_Omu]	24	COI (OK017074, OK017075, OK017077–OK017081, OK017083, OK017089, OK017091)*	Oda et al. 2022
		3	COI (XXXXXXXX–XXXXXXXX) 16S (XXXXXXXX–XXXXXXXX)	This study
X. ngatama	New Zealand	1	COI & 16S (KY985236)	Unpublished data

RESULTS

Morphological examination

As stated earlier, the only character that is able to separate the two species is whether an epibranchial tooth is present on the anterolateral margin (NK Ng et al. 2014). On the basis of the good series of specimens from Japan and near the type locality, it is clear the strength of the epibranchial tooth also varies among these specimens. While all large specimens do not have any trace of a tooth, the condition in smaller specimens is variable. In the holotype male and some specimens from the type locality at Nishino-shima-shinto (NSMT Cr. 5427) and along the same arc at Kita-Iwo-to Island (NSMT Cr. 33519–33544), the epibranchial tooth is present as a low tooth and separated from the margin by a shallow notch (Fig. 2A, C, D). In a paratype female and most of the specimens from these sites, the epibranchial tooth varies from very low to slightly crenulate to completely absent (Fig. 2B, E, F). In some specimens from Kita-Iwo-to Island (*e.g.*, female, 7.5 × 6.7 mm, NSMT Cr. 33520), the left anterolateral margin is slightly crenulate where the tooth should be, but the right anterolateral margin is entire without any trace of a tooth (Fig. 1F). The same is true of specimens from the Izu area (Fig. 3B). None of the specimens from Taiwan or Showa Iwo-Jima in southern Japan have a low tooth, but most have the margins slightly crenulate to entire (Fig. 3D–F). It is significant to note that the first crab stage of *X. testudinatus* possesses a small but distinct epibranchial tooth (Jeng et al. 2004b: fig. 5c), and this tooth becomes smaller, usually merging with the anterolateral margin as the crabs get larger. In summary, we conclude that the presence or absence of an epibranchial tooth is not useful to discriminate taxa.

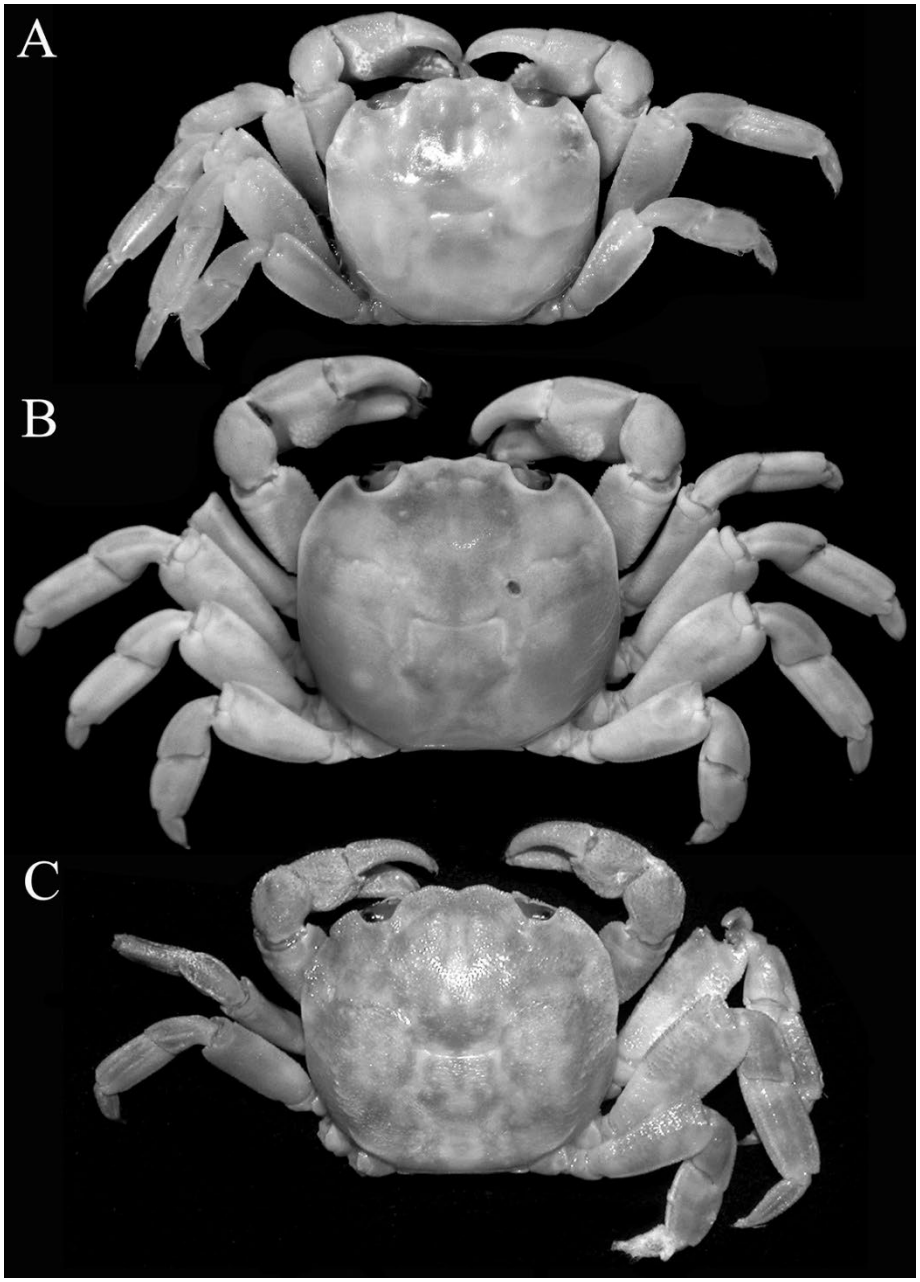

Fig. 1. A, *Xenograpsus novaeinsularis* Takeda & Kurata, 1977, holotype ♂ (7.3 × 6.4 mm), NSMT Cr. 5427; B, holotype of *Xenograpsus testudinatus* NK Ng, Huang & Ho, 2000, ♂ (19.9 × 18.4 mm), TMCD; C, *Xenograpsus ngatama* McLay, 2007, holotype, ♂ (16.0 × 15.6 mm), NIWA 18013.

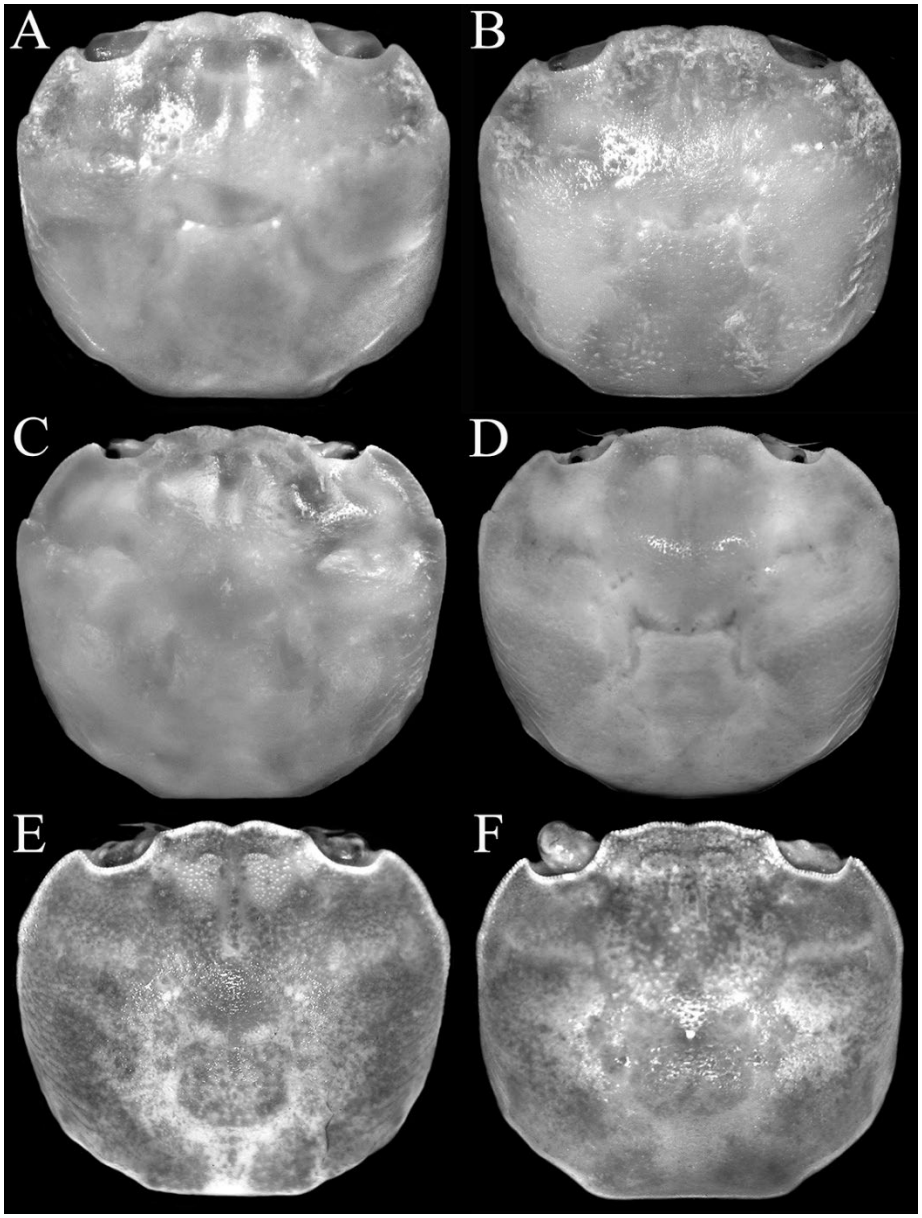

Fig. 2. *Xenograpsus novaeinsularis* Takeda & Kurata, 1977, dorsal view of carapace. A, holotype, ♂ (7.3 × 6.4 mm), Nishino-shima, NSMT Cr. 5427; B, paratype, ♀ (8.1 × 7.2 mm), Nishino-shima, NSMT Cr. 5473; C, ♂ (20.4 × 17.5 mm), Nishino-shima, NSMT Cr. 6570; D, ♂ (15.5 × 14.3 mm), Nishino-shima, ZRC 2008.1267; E, ♂ (14.2 × 12.9 mm), Kita-Iwo-to Island, NSMT Cr. 33519; F, ♀ (7.5 × 6.7 mm), Kita-Iwo-to Island, NSMT Cr. 33520.

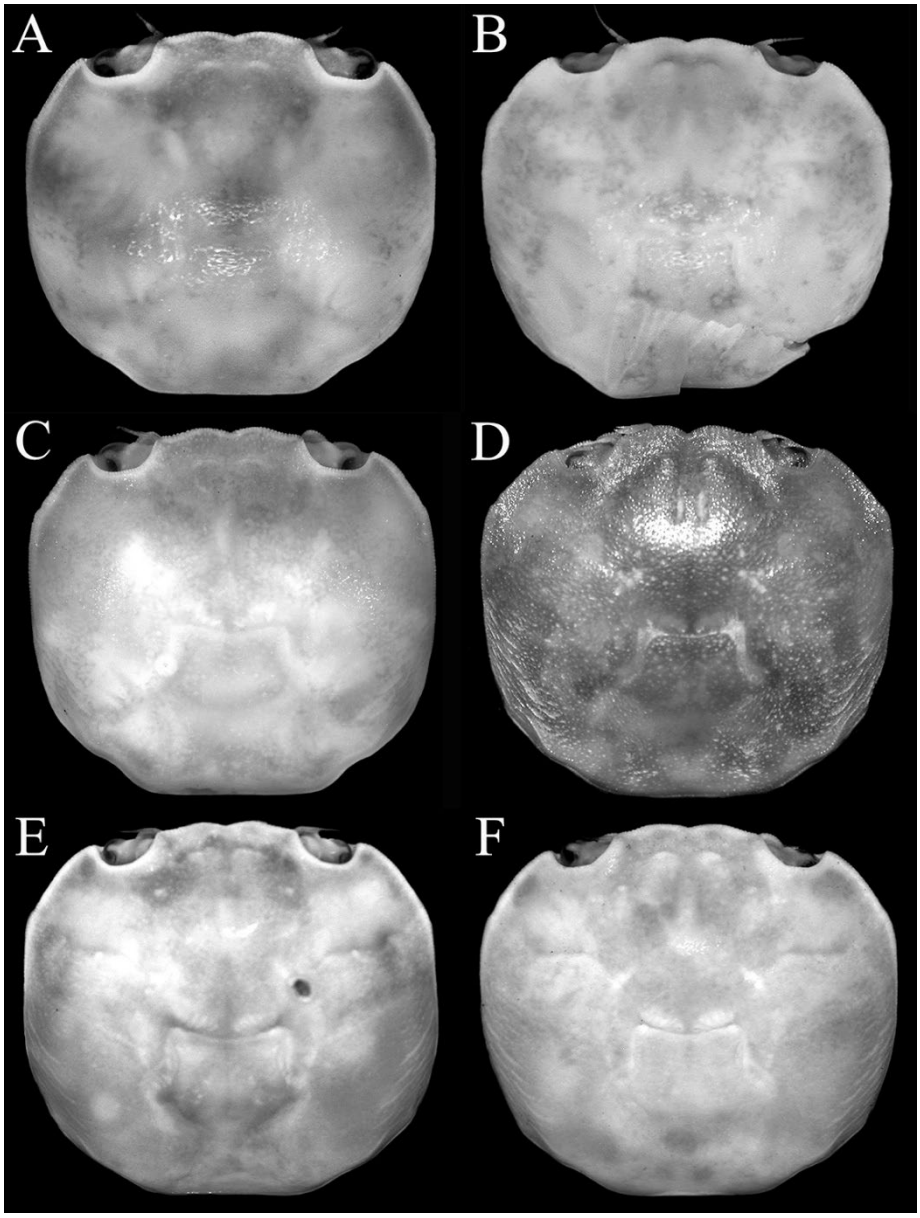

Fig. 3. *Xenograpsus novaeinsularis* Takeda & Kurata, 1977, dorsal view of carapace. A, ♂ (7.7 × 7.1 mm), Izu Islands, NSMT Cr. 33545; B, ♂ (12.4 × 11.2 mm), Izu Islands, NSMT Cr. 33546; C, ♀ (9.5 × 8.8 mm), Izu Islands, NSMT Cr. 33547; D, ♂ (16.1 × 14.3 mm), Showa Iwo-Jima, ZRC; E, ♂ (19.9 × 18.4 mm), holotype of *Xenograpsus testudinatus* NK Ng, Huang & Ho, 2000, Kueishan Island, TMCD; F, ♂ (15.8 × 14.4 mm), paratype of *Xenograpsus testudinatus* NK Ng, Huang & Ho, 2000, Kueishan Island, ZRC 2013.1824.

Txnonomy

Family Xenograpsidae NK Ng, Davie, Schubart and PKL Ng, 2007

Genus *Xenograpsus* Takeda & Kurata, 1977

Type species: *Xenograpsus novaeinsularis* Takeda & Kurata, 1977, by original designation.

Of the three species of *Xenograpsus* currently recognised, *X. testudinatus* Ng, Huang & Ho, 2000 is here synonymised under *X. novaeinsularis* Takeda & Kurata, 1977. *Xenograpsus ngatama*

McLay, 2007 is a distinct species from New Zealand waters and some aspects of its taxonomy need to be discussed. McLay (2007: 18–19) observed that "The three species of *Xenograpsus* are quite distinct from each other. *Xenograpsus novaeinsularis* from Japan and Marianas has well developed epigastric cristae, one prominent protogastric tubercle, anterolateral tooth present, oblique granulate crista absent on carapace above base of P5 and cervical groove prominent. *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 from Taiwan has the epigastric cristae well developed, one prominent protogastric tubercle, anterolateral tooth absent, oblique granulate crista present on carapace above base of P5 and cervical groove not prominent; while *X. ngatama* from New Zealand has epigastric tubercles not arranged in cristae, many large protogastric tubercles, anterolateral tooth present, oblique granulate crista present on carapace above base of P5 and a prominent cervical groove. A comparison of the many specimens of *X. novaeinsularis* with that of *X. ngatama* on hand (ZRC 2018.0195) as well as photographs of the type specimens the fourth author took when he examined them in Singapore, show that most of these characters do not work. The presence or absence of an epibranchial tooth, like in *X. novaeinsularis*, is not a useful character. In the ZRC specimen of *X. ngatama*, the right tooth is not visible (appears to be absent on the left as well but it is partly damaged) (Fig. 4B). Neither is the presence of well-developed oblique striae on the posterolateral surface (Fig. 4A, B); in some specimens of *X. novaeinsularis*, the striae can also be quite strong (Fig. 3D). The depth of the cervical groove is also not useful as any observed difference is minor at best. The epigastric crista of *X. ngatama* is indeed less pronounced with the surface covered with small granules and low striae but no obvious transverse crista is visible; and the protogastric region is covered with many small granules (Fig. 4A, B). In *X. novaeinsularis*, there is always a distinct epigastric crista, even if it is a bit low; and the protogastric region only has one distinct granule (sometimes absent) with the rest of the surface relatively smoother (Figs. 2, 3). Another character that appears to work well is the front – in *X. ngatama*, the frontal margin is prominently produced anteriorly, forming two distinctly convex lobes that are separated by a deep cleft (Fig. 4). In *X. novaeinsularis*, the frontal lobes are not strongly produced anteriorly, with the margins gently convex and the median cleft distinctly more shallow (Figs. 2, 3). The two species (herein we treated the four specimens from Kita-Iwo-to Island as *X. novaeinsularis*) are also genetically distinct, being separated by 13.0–13.9% and 5.2–5.9% on the sequences of mitochondrial CO1 and 16S rRNA genes respectively (Tables 2, 3).

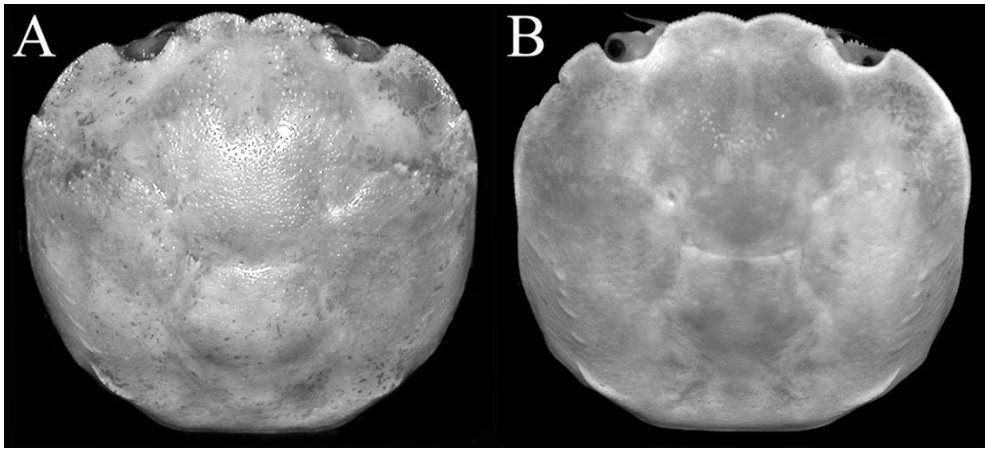

Fig. 4. *Xenograpsus ngatama* McLay, 2007, dorsal view of carapace. A, ♂ (27.1 × 25.8 mm), Kermadec Ridge, NIWA; B, ♂ (17.3 × 15.7 mm), Kermadec Ridge, ZRC 2018.0195.

***Xenograpsus novaeinsularis* Takeda & Kurata, 1977**

(Figs. 1–3)

Xenograpsus novaeinsularis Takeda and Kurata 1977: p. 100, figs. 6b, c, 7, 8 (Nishinoshima island); Takeda 1982: p. 216 (book); Takeda 1993: p. 80 (list); Takeda et al. 1993: p. 60 (Akuseki-jima, Tokara Islands and Kita-Iwo-to); Türkay and Sakai 1995: p. 33, figs. 7–9 (Mariana Arc); NK Ng et al. 2007: p. 239, fig. 2A (discussion); Giguere and Tunnicliffe 2021: S5 Table (Mariana Arc); Brunner et al. 2022: supplement (list); Takeda and Komatsu 2023: p. 174 (list).

Xenograpsus testudinatus NK Ng, Huang & Ho 2000: p. 192; figs. 1–3 (Kueishan Island); PKL Ng et al. 2001: p. 46 (list); NK Ng and Segonzac 2006: p. 474 (book); NK Ng et al. 2007: p. 239, figs. 2B, 3A–J, 4A, 5A, 6A, 7A (discussion); PKL Ng et al. 2008: p. 232 (list); NK Ng et al. 2014: p. 392, figs. 1, 2A, B (Kuchierabu-jima); PKL Ng et al. 2017: p. 116, fig. 14c (discussion); Suzuki et al. 2018: p. 87 (Kuchierabu-jima); Miyake et al. 2019: p. 32 (Shikine-jima Island); Yang et al. 2022: p. 7 (Kueishan Island and Kuchierabu-jima); Oda et al. 2022: p. 3 (Kueishan Island, Showa Iwo-jima, Shikine-jima, and Omuro-dashi).

Material examined: JAPAN: Holotype, male (7.3 × 6.4 mm), under volcanic debris, Nishino-shima-shinto, coll. Y Kurata, 25.VII.1975, NSMT Cr. 5427. Paratypes: same data as holotype, 1 female (8.1 × 7.2 mm), NSMT Cr. 5473; 1 male (5.7 × 5.0 mm), 1 ovigerous female (6.8 × 5.9 mm), NSMT Cr. 5474. Others: Nishino-shima-shinto, Tsukiura Wan, coll. Y Kurata and K Takenaga, 25.X.1979, 2 males (12.2 × 11.3 mm, 20.4 × 17.5 mm), NSMT Cr. 6570, 1 male (15.5 × 14.3 mm), ZRC 2008.1267; 1 male (13.0 × 11.3 mm), Ko-takara-jima, Tokara Retto, coll. Y Seyama, 2.V. 1998, NSMT Cr. 12440; hydrothermal vents, Funka-asane Bank, near Kita-Iwo-to Island, Ogasawara Arc, 25º26.95'N 141º14.62'E, 27 m, 29°C, coll. H Komatsu, SCUBA, 16–17. X. 2017, 16 males (5.4 × 5.0 mm – 17.7 × 16.2 mm), 8 females (5.1 × 4.5 mm – 8.9 × 8.1 mm), 2

ovigerous females (5.8 × 5.3 mm, 7.6 × 7.1 mm), NSMT-Cr 33519–33544, 1 male (10.8 × 9.7 mm), 1 female (7.4 × 6.6 mm), ZRC; Omuro-dashi submarine volcano, Izu Islands, 195–200 m, coll. H Komatsu, 16–18.V.2016, 9 males (6.4 × 5.7 mm – 12.4 × 11.2 mm), 1 young male (3.9 × 3.5 mm), 5 ovigerous females (7.0 × 6.3 mm – 9.5 × 8.5 mm), 14 females (6.1 × 5.5 mm – 9.9 × 9.1 mm), NSMT-Cr 33545–33573, 1 male (6.0 × 5.2 mm), ZRC, 1 ovigerous female (6.2 × 5.5 mm), ZRC; 62 males (5.3–22.9 × 5.0–20.6 mm), 18 females (6.7–15.5 × 6.1–14.0 mm), 14 ovigerous females (6.3–14.5 × 6.0–12.9 mm), 3 juveniles (5.0–5.4 × 4.5–4.8 mm), south of Showa Iwo-Jima (= Iōjima), Kagoshima Prefecture, 30º48.16'N 130º20.5'E, 3–5m, free hand collection, coll. K Furuta and S Dewa et al, 14.V.2011, ZRC 2025.2061. MARIANA ISLANDS: 11 males (5.6 × 4.9 mm – 12.3 × 11.2 mm), 7 ovigerous females (5.5 × 5.0 mm – 10.0 × 9.0 mm), North Esmeralda, North Mariana, North Pacific, coll. FS Sonne, 12.VII.1990, SMF 22945; 1 male (6.2 × 5.4 mm), 1 ovigerous female (5.6 × 4.7 mm), Esmeralda, North Mariana, North Pacific, 114 m, coll. FS Sonne, 21.VII. 1990, SMF 22946. TAIWAN: 1 male (19.9 × 18.4 mm), holotype of *Xenograpsus testudinatus* NK Ng, Huang & Ho, 2000, Gengxin Fish Port, Peikuan, 15 m depth in rocky reef, Ilan County, coll. P-H Ho, 3.X.1991, TMCD; paratypes of *Xenograpsus testudinatus* NK Ng, Huang & Ho, 2000, Gengxin Fish Port, Peikuan, 15 m depth in rocky reef, Ilan County, coll. P-H Ho, 3.X.1991, 1 male (21.7 × 20.1 mm), TMCD, 1 male (15.8 × 14.4 mm), ZRC 2013.1824, 1 male (17.8 × 16.3 mm), ZRC 2013.1825; off Kueishan Island, around hydrothermal vents, llan County, 16 m, diving, 18.IV.1999, 2 males (20.1 × 18.4 mm, 26.7 × 24.3 mm), 3 females (15.3 × 13.9 mm, 16.2 × 15.0 mm, 20.0 × 18.3 mm), ZRC 2022.0814, 6 males, 8 females, ASIZ 72ll6-2; stn CP114, 24°51.03'N 121°58.31'E, 128–250 m, 2.5 m beam trawl, 21.V. 2001, 1 male (26.8 × 23.7 mm), NTOU B00144; stn KS3, 24°49.22'N 121°59.57'E, 305 m, 2.5 m beam trawl, 12.VII. 2005, 1 male (26.3 × 24.5 mm), NTOU B00147; stn KS9, 24°50.66'N 121°59.70'E, 200 m, 2.5 m beam trawl, 13.VII. 2005, 12 males (12.9 × 11.5 mm – 24.3 × 21.9 mm), 6 females (16.5 × 15.5 mm – 23.7 × 21.6 mm), NTOU B00129; stn KS31, 24°49.68'N 122°00.25'E, 300 m, 2.5 m beam trawl, 4.IX.2008, 21 males (5.6 × 4.8 mm – 27.3 × 25.3 mm), 23 females (5.5 × 4.8 mm – 23.8 × 22.9 mm), NTOU B00142; stn KS32, 24°51.23'N 121°59.20'E, 252–275 m, 2.5 m beam trawl, 4.IV. 2008, 15 males (12.8 × 11.6 mm – 29.4 × 26.5 mm), 9 females (15.0 × 13.8 mm – 21.9 × 20.8 mm), NTOU B00131; stn KS40, 24°50.99'N 121°59.43'E, 224 m, 2.5 m beam trawl, 12.VIII.2010, 9 males (19.2 × 18.0 mm – 27.8 × 24.8 mm), 3 females (16.1 × 15.2 mm – 24.0 × 33.3 mm), NTOU B00145; stn KS41, 24°50.95'N 121°59.44'E, 224–232 m, 2.5 m beam trawl, 12.VIII.2010, 11 males (8.4 × 7.2 mm – 26.6 × 24.4 mm), 20 females (9.5 × 8.7 mm – 20.8 × 19.3 mm), NTOU B00143; collected by diving, 11.IX.2011, 42 males (6.8 × 5.8 mm – 28.1 × 25.5 mm), 14 females (10.5 × 9.6 mm – 25.4 × 22.3 mm), NTOU B00141; collected by diving, 10–15 m, 7.VIII.2013, 3 males (15.8 × 14.8 mm – 19.4 × 17.8 mm), 6 females (14.7 × 12.8 mm – 20.6 × 19.9 mm), NTOU B00128; collected by diving, 15–20 m, 12.VI.

2015, 9 males (28.1 × 25.3 mm – 23.1 × 21.1 mm), 8 ovigerous females (18.3 × 16.9 mm – 22.1 × 21.0 mm), 17 females (18.9 × 17.7 mm – 22.9 × 21.0 mm), NTOU B00146; coll. M-S Jeng, VIII.2000, 1 male (25.1 × 22.8 mm), 1 ovigerous female (16.1 × 15.2 mm), NSMT Cr. 13936.

Specimens for comparisons: *Xenograpsus ngatama* McLay, 2007: Holotype, male (16.0 × 15.6 mm), station KOK0505/43, Macauley Caldera, 30°2.06'S 181°17.36'E, 161 m, 15.IV. 2005, NIWA 18013. Paratypes: l male (19.7 × 19.0 mm), station KOK0505/45, Macauley Caldera, 30°2.16'S 181°17.63'E, 109 m, 16.IV. 2005, NIWA 18022; 1 female (12.8 × 11.7 mm), station KOK0505/49, Macauley Caldera, 30°2.0l'S 181°17.37'E, 156 m, 17.IV.2005, NIWA 18021. Others: 5 males (11.0 × 10.5 mm – 15.2 × 14.4 mm), station KOK0505/49, Macauley Caldera, 30°2.01'S 181°l 7.37'E, 156 m, 17.IV. 2005, NIWA 18020; Brothers Seamount, 35°44.22–44.04'S l78°29.72–29.63'E, 270–239 m, 21.V. 2001, 1 male (27.1 × 25.8mm), 1 male (missing carapace, estimated 44.1 × 42.0 mm), 1 female (34.8 × 33.1 mm, damaged, NIWA, 1 male (17.3 × 15.7 mm), ZRC 2018.0195; 2 males (16.8 × 15.3 mm, 17.8 × 16.5 mm), station TAN0411/10, northwest of Kermadec Ridge, 25°53.41–53.61'S 177°11.10–11.07'E, 139–236 m, 4.X. 2004, NIWA 18014.

Revised diagnosis: Carapace quadrate, almost rounded, slightly broader than long; surface finely granular, punctate; with visible posterolateral striations; glabrous; epigastric region raised, with distinct transverse granulated crista; protogastric region with single prominent granule. Frontal margin not strongly produced anteriorly, bilobed, with margins gently convex, median cleft relatively shallow. Anterolateral margins short, oblique, with single low epibranchial tooth or margin entire; posterolateral margins subparallel. Infraorbital border with large granules, deep incision at inner one-third; ridge below it with minute granules. Endostomial ridge prominent, granulated. Posterior margin of epistome entire, margin granulated, without lobulation. Male pleon triangular; telson triangular, widely elongated with rounded tip. G1 stout, heavily calcified, bearing subdistal outgrowth, distal fringe covered with setae. G2 short, with rounded tip. Vulva bluntly triangular in shape.

Distribution: Japan: Ogasawara Islands, northern Ryukyu Islands, Izu Islands, at depths of 5–200 m; in shallow volcanically active waters (Takeda and Kurata 1977; Takeda et al. 1993; NK Ng et al. 2014; Miyake et al. 2019; Oda et al. 2022). Mariana Islands: Mariana Arc, at depths of 63–114 m with hydothermal vents (Türkay and Sakai 1995; Giguère and Tunnicliffe 2021). Taiwan: Kueishan Island and northeastern areas, at depths of 10–323 m; generally associated with hydrothermal vents (Wang et al. 2014; Yang et al. 2022). The type locality of *X. novaeinsularis* is Nishino-shima-shinto (ca. 27°14.81'N 140°52.47'E), a volcanic landmass which has since joined with the main island of Nishino-shima and is now no longer regarded as a sepratae geographic entity. The recent specimens of *X. novaeinsularis* were collected from Funka-asane Bank, near

Kita-Iwo-to Island (25°26.95'N 141°14.62'E) and this site is about 200 km south-southeast of the type locality, along the same submarine volcanic arc.

Remarks: For the types of *Xenograpsus testudinatus*, the final repositories of some specimens have changed in the intervening years. The two male types from Gengxin Fish Port supposedly placed in NTOU and Smithsonian Institution (Washington DC) were retained in ZRC with the agreement of the authors of the species, and only two males and three females (not three males and four females) from Kueishan Island were transferred to the ZRC. *Xenograpsus ngatama* was described from 10 males and 2 females (but with only one holotype male and one paratype female) from five sites along the Kermadec Ridge (between 25°53'S–35°44'S and 181°17'E–177°11'E). McLay (2007: p.16) listed two males (27.1 × 25.8 mm, 44.1 × 42.0 (carapace missing) and one female (34.8 × 33.1 mm) from Brothers Seamount. The present male specimen (ZRC 2018.0195) has the same data as these three specimens but is not listed in his paper, its measurements (17.3 × 15.7 mm) being quite different. This specimen, together with the original specimens, were brought over to Singapore when the author visited in 2005 and he gifted the ZRC one specimen. McLay probably inadvertently forgot to include it in his material for the final paper.

DISCUSSION

NK Ng et al. (2007: p. 197) separated *X. testudinatus* from *X. novaeinsularis* by the absence of a epibranchial tubercle or tooth on the anterolateral margin of the carapace (versus with distinct epibranchial tooth); relatively more prominent epigastric cristae; more convex dorsal surface of the carapace; anteroexternal margin of the third maxilliped merus is weakly convex (versus strongly convex); cheliped merus is relatively shorter, with the length to width ratio 1.8 (versus relatively longer merus with a length to width ratio of 2.2); shorter and stouter ambulatory propodus, with a length to width ratio of 1.5 (versus length to width ratio 2.4); proportionately shorter and stouter ambulatory dactylus, with a length to width ratio of 2.3 (versus length to width ratio 3.8); lateral margins of ambulatory meri are subparallel (versus more convergent); distal margin of the male telson is broadly rounded (versus narrowly rounded); and G1 is more heavily calcified as well as proportionately shorter and stouter with a length to width ratio of 5.4 (versus relatively longer and more slender GI, with the length to width ratio 6.0).

Over the years since the original discovery, and with the study of hundreds of specimens of *X. testudinatus* (not all preserved), almost all the characters have been shown to be associated with size and/or variation (see NK Ng et al. 2007), and in the most recent

morphological appraisal, NK Ng et al. (2014) commented that the only character that can be used to separate the two species is the strength of the epibranchial tooth on the anterolateral margin – it is present in *X. novaeinsularis*, even if low, but is absent in *X. testudinatus*, with the margin appearing entire. This character is now also dismissed as the good series of Japanese specimens examined also show variation.

Comparing the molecular divergences between *X. novaeinsularis* (based on the samples from Kita-Iwo-to Islands in this study which are near the type locality) and *X. testudinatus*, the four tested individuals do not show distinctly intraspecific and interspecific differences with *X. testudinatus* from Taiwan and Japan in both the *COI* (intraspecific: 0.2–0.9%, interspecific: 0–1.7%, Table 2) and 16S rRNA (intraspecific: 0–0.2%, interspecific: 0–0.6%, Table 3) sequences. Even the genetic differentiations (F_{ST}) between *X. novaeinsularis* and *X. testudinatus* are not significant, although it is more significant for the 16S rRNA sequence between the deep-sea population of *X. testudinatus* in Taiwan versus the shallow water ones from Taiwan and Japan (Tables 2, 3). A total of 229 and 160 sequences on the mitochondrial *COI* and 16S rRNA genes represented 59 and 15 haplotypes, respectively. No population formed a unique grouping and even *X. novaeinsularis* from Kita-Iwo-to Islands shared the dominant haplotypes (Fig. 5). On the other hand, *X. ngatama* is quite different from *X. novaeinsularis* and *X. testudinatus*, and had undergone many genetic changes from the shallow-water population of *X. testudinatus*/ *X. novaeinsularis* (Fig. 5).

Table 2. Pairwise comparison of Kimura 2-parameters (K2P, below diagonal; range of same population is bolded on diagonal) genetic distances and F_{ST} index (above diagonal) based on COI gene (491–657 bp) dataset of *Xenograpsus* species. Numbers in parentheses mean the number of sequences on each population. Population abbreviations are listed in Table 1

	TD (70)	TS (56)	J_Ki (4)	J_Sho (61)	J_Shi (11)	J_Omu (27)	*X. ngatama*
TD (70)	**0–1.2**	0.00514	-0.08932	-0.00832	0.05127	-0.00721	0.94499
TS (56)	0–1.4	**0–1.4**	-0.08708	0.00972	-0.00333	-0.01270	0.93249
J_Ki (4)	0–1.1	0–1.2	**0.2–0.9**	-0.07651	-0.09878	-0.09980	0.92593
J_Sho (61)	0–1.7	0–1.7	0–1.6	**0–1.7**	0.06328	-0.00833	0.94977
J_Shi (11)	0–1.7	0–1.7	0–1.5	0–1.7	**0–1.4**	0.00618	0.94383
J_Omu (27)	0–1.9	0–1.9	0–1.7	0–1.9	0–1.7	**0–1.9**	0.93497
X. ngatama	12.8–14.2	12.8–14.0	13.0–13.9	10.7–14.0	11.7–12.1	10.7–14.0	-

Table 3. Pairwise comparison of Kimura 2-parameters (K2P, below diagonal; range of same population is bolded on diagonal) genetic distances and F_{ST} index (above diagonal) based on 16S rRNA gene (427–545bp) dataset of *Xenograpsus* species. Numbers in parentheses mean the number of sequences on each population. Population abbreviations are listed in Table 1. *, statistically significant with $P< 0.05$

	TD (70)	TS (52)	J_Sho (30)	J_Ki (4)	J_Omu (3)	*X. ngatama*
TD (70)	**0–0.6**	0.09694*	0.07687*	-0.13138	-0.20475	0.97125
TS (52)	0–0.6	**0–0.4**	-0.01582	-0.04545	0.03384	0.98981
J_Sho (30)	0–0.6	0–0.6	**0–0.4**	-0.07318	-0.01793	0.98720
J_Ki (4)	0–0.4	0–0.6	0–0.4	**0–0.2**	-0.38776	0.97980
J_Omu (3)	0–0.4	0–0.6	0–0.4	0–0.2	**0–0.2**	0.97297
X. ngatama	5.2–5.7	5.2–5.8	5.2–5.7	5.2–5.9	5.2–5.4	-

The underwater volcanic system in northern Taiwan is connected to a chain of shallow water hydrothermal vents and systems reaching to the Izu area south of Tokyo and continues to the Ogasawara (= Bonin) Islands (the Izu-Bonin Arc), and reaching further south into the Mariana Arc (see Brunner et al. 2022). The larvae of *X. novaeinsularis* are known to be planktonic (Jeng et al. 2004b; Dahms et al. 2017) and as such can easily be dispersed by surface and subsurface currents. Moreover, the species has a wide vertical depth range from 5 m to at least 323 m (NK Ng et al. 2014; Wang et al. 2014) and this only further enhances its dispersal abilities. The major system in that area is the Kuroshio Current, a strong warm-water surface system that flows northwards along the western section of the North Pacific Ocean Basin and is part of the subtropical North Pacific Gyre (Imawaki et al. 2001). Oda et al. (2022) discussed at length possible dispersal via the Kuroshio Current, and this well-known oceanographic system explains how *X. novaeinsularis* occurs from Taiwan to the Mariana Arc, with minimal genetic divergence (see also Tsang et al. 2022).

The diet of *Xenograpsus* species is not restricted to vent fauna and marine snow (cf. Jeng et al. 2004b), and is relatively varied (cf. Comeault et al. 2010; Ho et al. 2015; Yang et al. 2016, Chang et al. 2018; Wang et al. 2022). Giguere and Tunnicliffe (2021) included *X. novaeinsularis* in their study of beta diversity and conservation in the Mariana Arc and Back-Arc systems (see also Brunner et al. 2022).

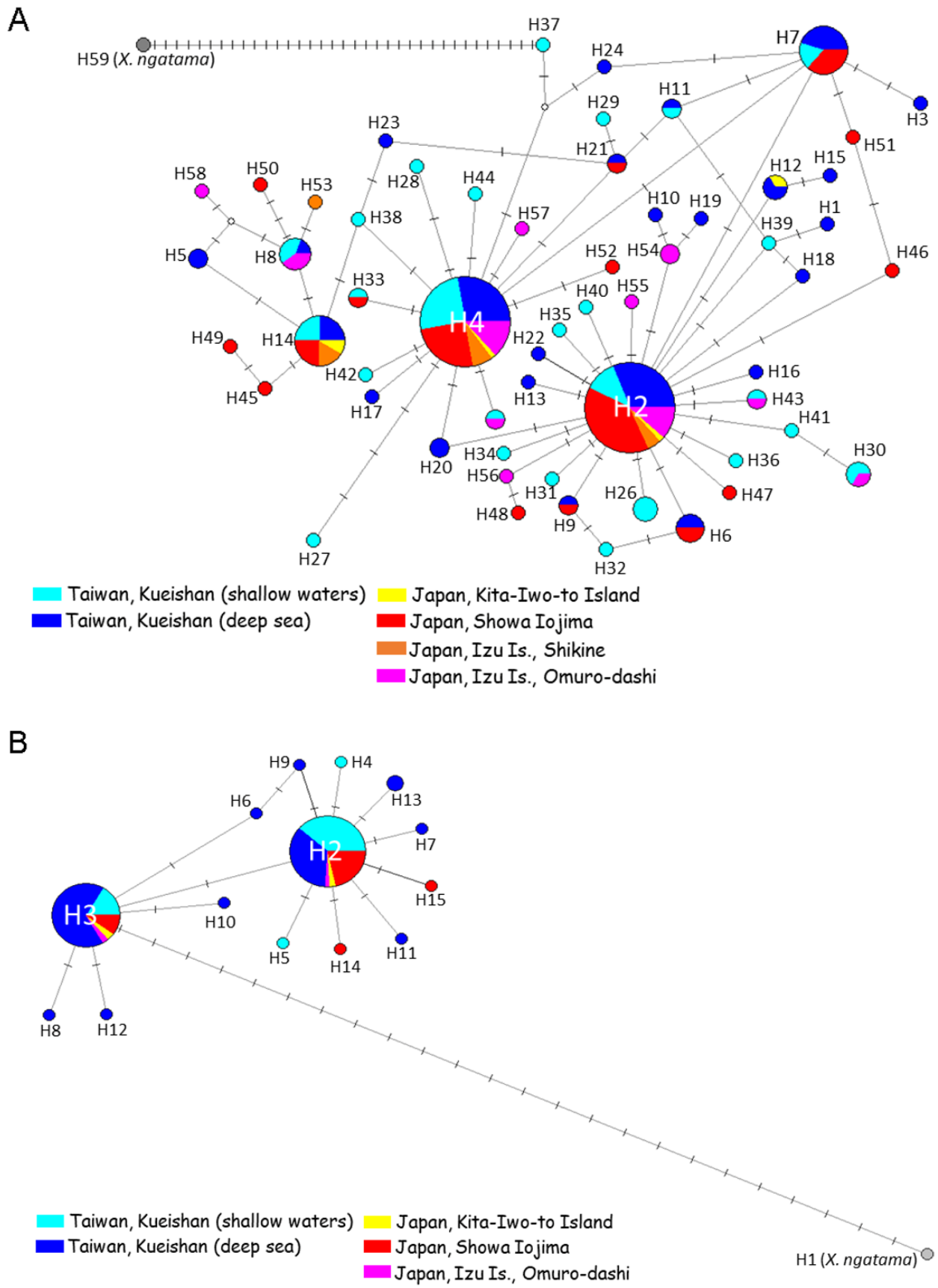

Fig. 5. Median-joining networks constructed from: A, 59 haplotypes on COI gene and; B, 15 haplotypes 16S rRNA gene dataset of *Xenograpsus* species among different populations in Taiwan

and Japan. *X. ngatama* McLay, 2007 was treated as outgroup. Size of circle corresponding to relative numbers for each haplotype.

Key to species of *Xenograpsus*

1a. Carapace with transverse epigastric crista distinct; usually with a distinct protogastric granule, region otherwise smooth or almost so; frontal lobes not strongly produced anteriorly, with margins gently convex and median cleft relatively shallow ……..…..... *X. novaeinsularis* Takeda & Kurata, 1977 (shallow water volcanic arcs in Taiwan to Japan and Marianas)

1b. Carapace with epigastric region raised but covered with low granules and striae, no obvious transverse crista visible; many small protogastric granules; frontal margin prominently produced anteriorly, forming 2 distinctly convex lobes separated by deep cleft ..…... *X. ngatama* McLay, 2007 (volcanic arcs in Kermadec Ridge, New Zealand)

CONCLUSIONS

The hydrothermal vent crab *Xenograpsus testudinatus* (Xenograpsidae) has been received substantial attention in Taiwan for over two decades, and there a substantial amount of research has been conducted on this crab by many scientists. In this study, *X. testudinatus* is verified to an actually junior synonym of *X. novaeinsularis* using integrated taxonomy that combines morphological comparisons and molecular analyses on a large series of Japanese and Taiwanese specimens, including from the type locality. Therefore, the name of this crab needs to be changed to *X. novaeinsularis.*

Acknowledgments: This paper started over a decade ago, when the fourth author in this work, together with the late Ng Ngan Kee realised that *X. testudinatus* was likely to be synonymous with *X. novaeinsularis* as their study of numerous specimens showed no major morphological differences between them. The failure to get fresh material and tissues of *X. novaeinsularis* from the type locality for DNA analysis meant that the final necessary piece of molecular evidence was missing; and this prevailed until the first author managed to recently obtain fresh material from near Nishino-shima-shinto. We also thank Tohru Naruse for helping us with various aspects of the study.

Authors' contributions: HK collected the samples from Japan, provided the initial molecular datasets and initiated analysis to suggest conspecificity. CHY conducted the detailed analyses of

molecular datasets, revised the final manuscript and wrote many parts of the text. TYC and PKLN reappraised the morphological characters of the samples and finalised the main discussion.

Competing interests: All authors declare that they have no conflict of interest.

Availability of data and materials: DNA sequences generated in the study have been deposited in the GenBank (NCBI).

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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