

The identity of the iconic Japanese ‘Heike-gani’,
Heikeopsis japonica (von Siebold, 1824)
(Crustacea, Decapoda, Brachyura, Dorippidae)

Danièle GUINOT, Peter K. L. NG,
Tohru NARUSE & Valentin de MAZANCOURT

DIRECTEUR DE LA PUBLICATION / *PUBLICATION DIRECTOR*: Gilles Bloch
Président du Muséum national d'Histoire naturelle

RÉDACTRICE EN CHEF / *EDITOR-IN-CHIEF*: Laure Desutter-Grandcolas

ASSISTANTE DE RÉDACTION / *ASSISTANT EDITOR*: Anne Mabilille (zoosyst@mnhn.fr)

MISE EN PAGE / *PAGE LAYOUT*: Anne Mabilille

COMITÉ SCIENTIFIQUE / *SCIENTIFIC BOARD*:

Nesrine Akkari (Naturhistorisches Museum, Vienne, Autriche)
Maria Marta Cigliano (Museo de La Plata, La Plata, Argentine)
Serge Gofas (Universidad de Málaga, Málaga, Espagne)
Sylvain Hugel (CNRS, Université de Strasbourg, France)
Marco Isaia (Università degli Studi di Torino, Turin, Italie)
Rafael Marquez (CSIC, Madrid, Espagne)
Jose Christopher E. Mendoza (Lee Kong Chian Natural History Museum, Singapour)
Annemarie Ohler (MNHN, Paris, France)
Jean-Yves Rasplus (INRA, Montferrier-sur-Lez, France)
Wanda M. Weiner (Polish Academy of Sciences, Cracovie, Pologne)

COUVERTURE / *COVER*:

Colour print by Utagawa Kuniyoshi in 1851: closeup of the 'Heike-gani' or 'samurai crab', during the naval battle at Dan-no-ura (1185) in Japan's Inland Sea.

Zoosystema est indexé dans / *Zoosystema is indexed in*:

- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus®

Zoosystema est distribué en version électronique par / *Zoosystema is distributed electronically by*:

- BioOne® (<http://www.bioone.org>)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Zoosystema* sont référencés par /
Articles and nomenclatural novelties published in Zoosystema are referenced by:

- ZooBank® (<http://zoobank.org>)

Zoosystema est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris / *Zoosystema is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish*:

Adansonia, Geodiversitas, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie, Comptes Rendus Palevol*.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2024
ISSN (imprimé / *print*): 1280-9551/ ISSN (électronique / *electronic*): 1638-9387

The identity of the iconic Japanese ‘Heike-gani’, *Heikeopsis japonica* (von Siebold, 1824) (Crustacea, Decapoda, Brachyura, Dorippidae)

Danièle GUINOT

Institut de Systématique, Évolution, Biodiversité (ISYEB)
Muséum national d’Histoire naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles
Case postale 53, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
daniele.guinot@mnhn.fr

Peter K. L. NG

Lee Kong Chian Natural History Museum, Conservatory Drive,
National University of Singapore, Singapore 117377 (Republic of Singapore)
peterng@nus.edu.sg

Tohru NARUSE

Tropical Biosphere Research Center, Iriomote Station
University of the Ryukyus, 870 Uehara, Taketomi, Okinawa 907-1541 (Japan)
naruse@lab.u-ryukyu.ac.jp

Valentin de MAZANCOURT

Laboratoire de Biologie des Organismes et Écosystèmes Aquatiques (BOREA)
Muséum national d’Histoire naturelle, CNRS, IRD, Sorbonne Université,
Université de Caen Normandie, Université des Antilles,
Case postale 26, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
valentin.demazancourt_ext@mnhn.fr

Submitted on 12 March 2024 | Accepted on 13 May 2024 | Published on 10 December 2024

Dedicated to Lipke B. Holthuis and Raymond B. Manning

urn:lsid:zoobank.org:pub:1C5C17AD-CBFA-4F51-A856-2D0CE191ABEC

Guinot D., Ng P. K. L., Naruse T. & de Mazancourt V. 2024. — The identity of the iconic Japanese ‘Heike-gani’, *Heikeopsis japonica* (von Siebold, 1824) (Crustacea, Decapoda, Brachyura, Dorippidae). *Zoosystema* 46 (31): 775-811. <https://doi.org/10.5252/zoosystema2024v46a31>. <http://zoosystema.com/46/31>

ABSTRACT

In the Dorippidae H. Milne Edwards, 1837, as revised by Holthuis & Manning (1990), ambulatory leg length, which is often utilised as a criterion for specific morphological differentiation, has proved to be a reliable character, even for the few cases where sexual dimorphism is observed in relative lengths. However, the discrepancies in the use of ambulatory leg length by these authors in the case of the iconic East Asian crab *Heikeopsis japonica* (von Siebold, 1824) is an issue that requires detailed study. The use of ambulatory leg length in dorippids has since been followed up by other researchers, but it is clear that there is a problem with this species. The taxonomy of the Heike-gani crab is therefore examined here in depth. In their revision, Holthuis & Manning (1990) did not discuss or resolve the problem that in *H. japonica* the first and second ambulatory legs are constantly and consistently long and narrow in adults of both sexes for most specimens in Japan, Taiwan and southern China, whereas the populations from the North China Sea have legs that are usually distinctly shorter and wider. Holthuis & Manning (1990) synonymised the long-legged *Neodorippe* (*Neodorippe*) *japonica* var. *taiwanensis* Serène &

KEY WORDS
Morphological variability,
ambulatory leg length,
long-legged morph,
short-legged morph,
Neodorippe (Neodorippe)
japonica var. *taiwanensis*,
Heikea arachnoides,
incipient speciation,
molecular analysis,
16S rRNA,
East Asia

Romimohtarto, 1969 with *Heikea japonica* (von Siebold, 1824) but, in addition, recognised a new very long-legged species from the Inland Sea in Japan, *H. arachnoides* (Manning & Holthuis, 1986). While the first and second ambulatory legs of *H. arachnoides* are relatively longer than in the typical *H. japonica* from the other parts of Japan, the difference is slight, and the holotype is not a fully adult specimen. Much of the literature on *H. japonica* from Japan, China, Hong Kong, Taiwan, and Korea does not discriminate between the leg lengths, and most authors follow the prognosis of Holthuis & Manning (1990) for the taxonomy. To better understand the problem with leg lengths in *H. japonica*, we examined a large series of specimens of these different leg-morphs from across its distribution, including the types of the various taxa. We confirm here that *Neodorippe (Neodorippe) japonica* var. *taiwanensis* is a junior synonym of *H. japonica* s. str. We also show that *Heikea arachnoides* Manning & Holthuis, 1986, based on not fully-grown individuals, is clearly a junior synonym of *H. japonica* s. str. as we demonstrate here that subadults and juveniles usually have proportionately longer and more slender first and second ambulatory legs. Notably, while all adult specimens from northern Chinese waters have shorter legs in contrast to those from other areas, this character is not unique to them: there were some specimens from Japan, Taiwan and southern China that possess relatively shorter legs as well, and others that belonged to the typical long-legged morph. Detailed morphological examination (including gonopods) of hundreds of specimens and analysis of sequence data for the mitochondrial 16S rRNA gene did not reveal any significant characters that could be used to separate the two morphs. This may be one of the very first cases of incipient speciation or cladogenesis taking place in a widely distributed species, with the northern Chinese population beginning to be isolated, but not long enough for other morphological and/or genetic characters to manifest themselves.

RÉSUMÉ

L'identité du crabe japonais iconique «Heike-gani», Heikeopsis japonica (von Siebold, 1824) (Crustacea, Decapoda, Brachyura, Dorippidae).

Chez les Dorippidae *H. Milne Edwards*, 1837, tels que révisés par Holthuis & Manning (1990), la longueur des pattes ambulatoires, souvent utilisée comme critère de différenciation morphologique spécifique, s'est avérée être un caractère fiable, même dans les rares cas où un dimorphisme sexuel est observé dans les longueurs relatives. Cependant, les divergences dans l'utilisation de la longueur des pattes ambulatoires par ces auteurs dans le cas du crabe emblématique d'Asie orientale *Heikeopsis japonica* (von Siebold, 1824) est une question qui nécessite une étude détaillée. La longueur des pattes ambulatoires a continué à être utilisée par d'autres chercheurs, mais il est clair qu'il y a un problème avec cette espèce. La taxonomie du crabe Heike-gani est donc examinée ici en détail. Dans leur révision, Holthuis & Manning (1990) n'ont pas discuté ni résolu le problème selon lequel chez *H. japonica* les première et deuxième pattes ambulatoires des adultes des deux sexes sont constamment et régulièrement longues et étroites chez la plupart des spécimens du Japon, de Taiwan et de Chine du Sud, alors qu'elles sont généralement nettement plus courtes et plus larges dans les populations de la mer de Chine du Nord. Holthuis & Manning (1990) ont mis en synonymie *Neodorippe (Neodorippe) japonica* var. *taiwanensis* Serène & Romimohtarto, 1969 avec *Heikea japonica* (von Siebold, 1824) et, en outre, ont reconnu une nouvelle espèce à très longues pattes dans la Mer intérieure du Japon, *H. arachnoides* (Manning & Holthuis, 1986). Bien que les première et deuxième pattes ambulatoires de *H. arachnoides* soient relativement plus longues que celles de l'espèce typique *H. japonica* d'autres régions du Japon, la différence est faible, et l'holotype n'est pas un spécimen complètement adulte. Une grande partie de la littérature concernant *H. japonica* du Japon, de Chine, de Hong Kong, de Taiwan et de Corée ne fait pas de distinction entre la longueur des pattes, et la plupart des auteurs suivent la diagnose de Holthuis & Manning (1990). Pour mieux comprendre le problème de la longueur des pattes chez *H. japonica*, nous avons examiné une grande série d'individus des différents morphes de pattes provenant de l'ensemble de sa distribution, y compris les types des différents taxons. Nous pouvons confirmer que *Neodorippe (Neodorippe) japonica* var. *taiwanensis* est un synonyme junior de *H. japonica* s. str. Nous montrons également que *Heikea arachnoides* (Manning & Holthuis, 1986), décrit sur la base d'individus n'ayant pas atteint leur maturité, est indubitablement un synonyme junior de *H. japonica* s. str. car il est démontré ici que les subadultes et les juvéniles ont généralement les première et deuxième pattes ambulatoires proportionnellement plus longues et plus fines. Malheureusement, alors que tous les spécimens adultes des eaux du nord de la Chine ont des pattes plus courtes que ceux des autres régions, ce caractère ne leur est pas exclusif : quelques spécimens du Japon, de Taiwan et du sud de la Chine possèdent également des pattes relativement plus courtes, bien que la plupart d'entre eux appartiennent au morphe typique à longues pattes. Un examen morphologique détaillé (y compris des gonopodes) de centaines d'individus et l'analyse des données de séquence du gène mitochondrial ARNr 16S n'ont pas permis de révéler de caractères significatifs pouvant être utilisés pour distinguer les deux morphes. Il pourrait s'agir de l'un des tout premiers cas observés de spéciation ou de cladogenèse naissante chez une espèce largement répandue, la population du nord de la Chine étant au début du processus d'isolement, mais pas depuis assez longtemps pour que d'autres caractères morphologiques et/ou génétiques apparaissent.

MOTS CLÉS
Variabilité morphologique,
pattes ambulatoires,
forme à pattes longues,
forme à pattes courtes,
Neodorippe (Neodorippe)
japonica var. *taiwanensis*,
Heikea arachnoides,
cladogenèse,
analyse moléculaire,
ARNr 16S,
Asie de l'Est.

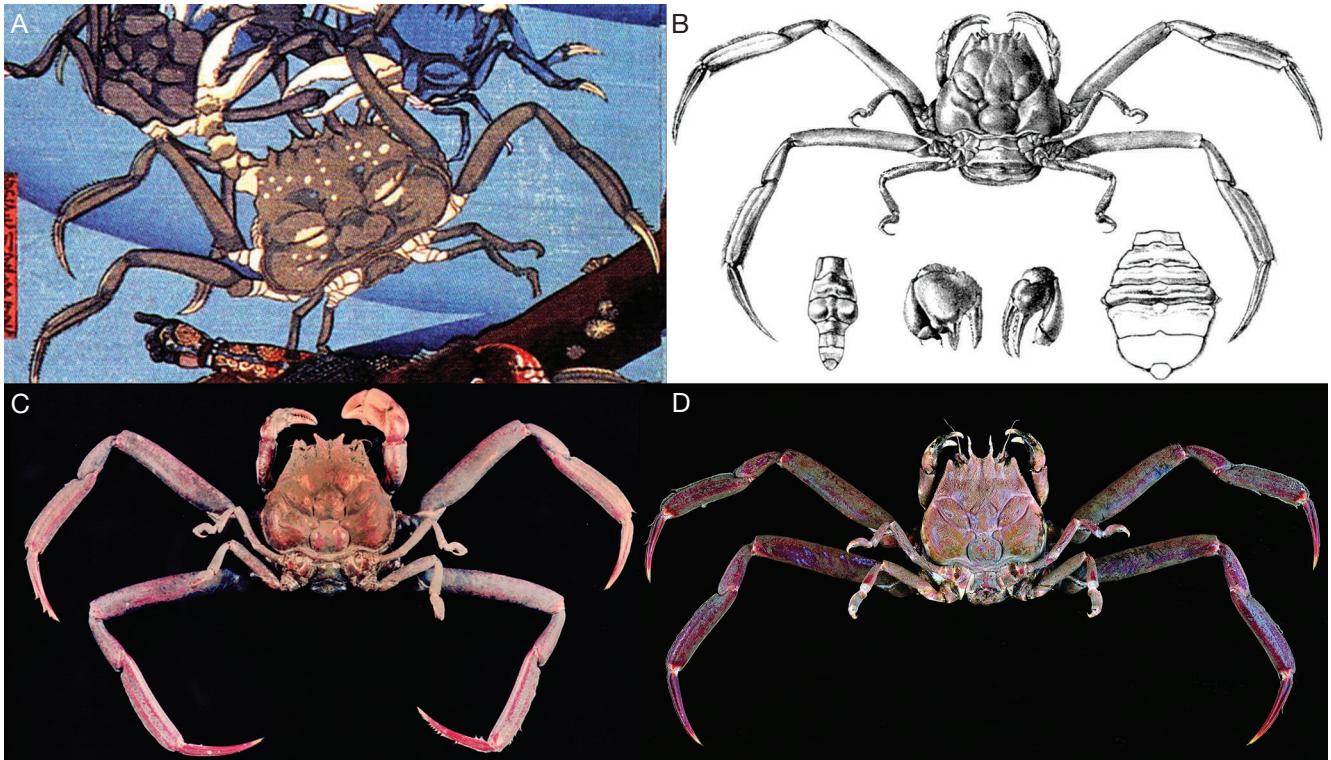


FIG. 1. — *Heikeopsis japonica* (von Siebold, 1824), typical morph: **A**, Colour print by Utagawa Kuniyoshi in 1851: closeup of the ‘Heike-gani’ or ‘samurai crab’, during the naval battle at Dan-no-ura (1185) in Japan’s Inland Sea; **B**, after De Haan (1839: pl. 31, fig. 1); **C**, ♂ 23.9×27.5 mm, Tashi, Ilan, Taiwan, coll. J.-F. Huang, NTOU 8910-06-37 [not examined] [photograph courtesy of J.-F. Huang]; **D**, ♂, Tashi, Ilan, Taiwan, coll. T.-Y. Chan [specimen not preserved; photograph courtesy T.-Y. Chan].

INTRODUCTION

Heikeopsis japonica (von Siebold, 1824) was described by von Siebold (1824: 14, footnote 3; 1826: 18; 1850: viii, as *Dorippe japonica*). In his *Commentatio*, von Siebold (1850: xi) explains that, having just arrived in Japan in 1823, he had been welcomed by the ‘presiding officer’ of Dutch trade J. Cock Blomhoff, who had already collected “for us [...] with energy and liberality rarer Crustacea, whether remarkable in form or size”. And the result was the “little work, printed in the year 1824 at Batavia”, that “contains the first published systematic enumeration of Japanese crustaceans, and therefore has some historical value”. This explains the remarkably fast publication of the paper soon after von Siebold’s arrival in Japan. The species was figured and studied in *Fauna Japonica* by De Haan (1839: pl. 31, fig. 1, as *Dorippe japonica*; 1841: 122, as *D. callida*; in Index p. 237, as *D. japonica*). Von Siebold (1824: 14), De Haan (1841: 122) and von Siebold (1850: viii, footnote, xi) gave *Dorippe japonica* the vernacular names ‘Heike-gani’, ‘Heike-Kani’ and ‘Feike-Gani’, respectively, with von Siebold and De Haan explaining: ‘Heike is the name of an emperor of Antiquity’ (*Heike est nomen imperatoris antiqui*) (see Holthuis & Sakai 1970: 116). The Heike (House of Taira) was actually one of the four most important clans during Heian period. In his *Commentatio physico-historica de Crustaceis Japonicis*, von Siebold (1850: viii) alludes to this noble family (which he names Feike) and

their members who perished at sea in 1185, whom the local inhabitants believe transformed into crabs, recognisable by the face-like patterns on the crabs’ carapace. (Fig. 1A) (see also Takoshima 2016). The mythology associated with the species has been well elaborated on by many workers (see Holthuis & Manning 1990; Martin 1993; Guinot 2023). The discovery of this emblematic Japanese crab is very interesting because it merges with the new era for Japanese zoology, for which von Siebold laid the foundations with his outstanding *Fauna Japonica*, published between 1833 and 1850 (see Holthuis 1953 for the date of publication of its different parts).

In a preliminary paper, Manning & Holthuis (1986) described four new species of dorippids, including a long-legged species from western Japan (Inland Sea) based on a single specimen, *Nobilum arachnoides*. Holthuis & Manning (1990) then revised the family and established a new genus, *Heikea*, for *Dorippe japonica* von Siebold, 1824. They have synonymised *Neodorippe* (*Neodorippe*) *japonica* var. *taiwanensis* Serène & Romimohtarto, 1969 under *Heikea japonica*, and transferred *Nobilum arachnoides* to *Heikea*, so that, as a result, two species are currently recognised in Japan and Taiwan: the typical *Heikeopsis japonica* and *H. arachnoides* (Manning & Holthuis, 1986). Ng *et al.* (2008) noted that the name *Heikea* was preoccupied by a fossil mollusc name (Isberg 1934) and proposed the replacement name *Heikeopsis*. Guinot (2023) subsequently revised the classification of the Dorippidae and

placed *Heikeopsis* and *Nobilum* Holthuis & Manning, 1990, as well as *Neodorippe* Serène & Romimohtarto, 1969, in a new subfamily, the Heikeopsinae.

The female that De Haan illustrated and described as *Dorippe Japonica* in *Fauna japonica* (De Haan 1839: pl. 31, fig. 1; 1841: 122: ‘legs scarcely four times as long as carapace’), reproduced by Holthuis & Manning (1990: fig. 34, as *Heikea japonica*) and Guinot (2023: fig. 1A), has very long and slender first and second ambulatory legs. The lectotype and paralectotypes selected and figured by Yamaguchi & Baba (1993: 300: fig. 90-A, B) have the meri of the first and second ambulatory legs thin and long, and much longer than the length of the carapace.

Heikeopsis japonica is a common species in Japan, especially in relatively shallow waters with muddy substratum, i.e., Inland Sea, Ariake Bay (Sakai 1976; 1985; Takeda *et al.* 2011), and the numerous specimens we have examined from Japan are all of this form. Almost all Japanese specimens of both sexes that have been figured and we have examined conform to this specification. While the first and second ambulatory legs of some females appear to be slightly shorter and stouter than those of males in some samples, there is no obvious pattern, and we conclude that the leg characters do not show substantial variability between sexes in this species. Interestingly, the Heike-gani or ‘samurai crab’ painted in the 1800s by Utagawa Kuniyoshi (Guinot 2023: figs 2, 39) have elongated, slender first and second ambulatory legs, in contrast to the very reduced and dorsally carried P4 and P5 (Fig. 1A).

As mentioned by Guinot (2023), there is a problem with the identity of *Heikeopsis japonica* in other parts of its range. Almost all specimens from northern China (from literature and those we have examined) identified with *Heikeopsis japonica* differ from the typical *H. japonica* from Japan and Taiwan in having relatively shorter and more robust first and second ambulatory legs. In his key paper ‘Heike-gani, its Prosperity and Fossils’, Sakai (1985: 330, 331, 333, 336) had already noted a discrepancy when he reproduced in his fig. 1 the figure of the specimen represented by De Haan that is the typical morph of *Dorippe japonica* with long and slender first and second ambulatory legs; and next to, in his fig. 3 (at the top), the figure of *Dorippe japonica* by Shen (1932: fig. 6) showing a crab from North China with its short and stout first and second ambulatory legs. Holthuis & Manning (1990) did not discuss this at all in their revision of the Dorippidae, although they figured both the long-legged Japanese De Haan’s 1939 specimen and the short-legged northern Chinese specimen of Shen (1932) (see Holthuis & Manning 1990: figs 34, 35, respectively) without discriminating or discussing them. In their redescription of *H. japonica*, Holthuis & Manning (1990: 80) defined the species only as: “Second and third legs slender, long, both reaching beyond front [of carapace] with distal end of merus”, ignoring the short-legged morph, and included in their *Heikea japonica* material from Japan, China, Taiwan, Korea, Vietnam and the Paracel Islands.

Holthuis & Manning’s (1990) treatment of *Heikeopsis japonica* is hard to explain but it is probably connected to their decision to recognise their new species, *H. arachnoides*

(Manning & Holthuis, 1986), from the Inland Sea, near Kobe, western Japan. Given that Holthuis & Manning (1990: 3) refer to the chelipeds or first pereopods as P1 and the walking legs as P2 to P5, they write:

“It was with some hesitation that we named this species, which is very similar to *H. japonica*, differing in having much slenderer and longer third pereopods, especially since this was the feature used by Serène & Romimohtarto (1969) to distinguish their *Neodorippe japonicum taiwanensis* from *N. japonicum* proper. In *H. arachnoides* the merus of the third leg [P3] is 6.6 to 7.3 times longer than high, whereas in material of *H. japonica* examined by us the third leg is 4.0 to 6.3 times longer than high; in the majority of specimens examined it is less than 6 times longer than high. In the specimens reported by Serène & Romimohtarto (1969) the merus was 5.9 times longer than high in their var. *taiwanensis*, 5.3 times in their *japonicum sensu stricto*.” (Holthuis & Manning 1990: 75).”

Their decision was therefore based on dividing all their specimens of *Heikea japonica* into two major morpho-groups based on the proportions of the second ambulatory leg merus. The group that they consider having proportionately “shorter” legs (i.e., the merus of the second ambulatory leg is 4.0–6.3 times) they treat as *H. japonica* s. str.; the group with “longer” legs (i.e., merus of the second ambulatory leg is 6.6–7.3 times), which was only known from three specimens from the Inland Sea of Japan, they called *H. arachnoides*. Why they decided on the division point between 6.3 and 6.6 is hard to understand, as the specimens with distinctly shorter ambulatory legs in northern China actually stand out more. The crabs depicted in Japanese literature generally have relatively long, slender legs, although this is not always reliable as we cannot ascertain how they were photographed or drawn (i.e., whether the first and second ambulatory legs were relatively flat when they were depicted or whether they were viewed at an angle). For example, the watercolours by Tune Sakai usually show a male crab with long, slender first and second ambulatory legs (e.g., Sakai 1937: pl. 10, fig. 1), but his later figure of another specimen has shorter legs (Sakai 1976: pl. 22, fig. 1). Figures by Miyake (1983: pl. 6, fig. 1), Takeda (1982: 121, coloured figure), Takeda (1983: 120, complete coloured figure), Yamaguchi *et al.* (1987: pl. 1, fig. 10), Guinot (2023: figs 1, 19A–C) all show crabs with longer first and second ambulatory legs. The first and second ambulatory legs of the megalopa of *H. japonica* are also very slender and those of the first crab are as long as 3 times (first ambulatory leg) or 3.5 times (second ambulatory leg) the carapace length (Quintana 1987: 253, figs 8C, 12G, as *Nobilum japonicum japonicum*). In the intervening years, carcinologists have followed the conclusions of Holthuis & Manning (1990) about *Heikeopsis japonica* and *H. arachnoides*. Later reports (e.g. Ng & Huang 1997; Chen & Sun 2002; Wong *et al.* 2021) have reported *H. arachnoides* from Taiwan and China, mainly on the basis of the longer second ambulatory leg.

Serène & Romimohtarto (1969: 14, figs 21, 22, pl. 5A, B, D) established *Neodorippe (Neodorippe) japonica* var.

taiwanensis for two specimens from Keelung, Taiwan, with the second ambulatory leg having a total length (coxa and basis-ischium excluded) 3.2 times the carapace length, thus longer and slimmer than that of the Chinese specimens, and almost similar to that of the Japanese specimens. Holthuis & Manning (1990: 87) have, however, synonymised the two taxa as noted above. It is important to note that Serène & Romimohtarto (1969: 5, key, 13, as *Neodorippe* (*Neodorippe*) *japonica*) had already recognised (with some doubt) that the Shen’s northern Chinese specimen (Shen 1932) was a ‘*N. japonica*’, arguing that its second ambulatory leg was “less than 3 times the length of carapace instead of a few more than 3 times on *japonica*, and a merus 4.5 times as broad as long instead of more than 5 times” on their material (from Vietnam and Japan) and on the Japanese large male specimen from Onomiti (Onomichi, Hiroshima Prefecture, on the coast of the Inland Sea) illustrated by Sakai (1937: 72, pl. 10, fig. 1, as *Dorippe japonica*). Serène & Romimohtarto (1969: 13) calculated that for Shen’s specimen (1932) the ratio of the length of the second ambulatory leg to the length of carapace was 3.27 for the male and 2.86 for the female, and that the ratio was 2.83 for the length of the first ambulatory leg to the length of the carapace. In contrast, the ratio was more than 3.6 in the specimen of Serène & Romimohtarto (1969) and was 3.4 for the first ambulatory leg in the Sakai’s specimen (1937).

In other dorippid species, where the first and second ambulatory legs are always relatively long, the relative length of the merus proves to be a reliable specific character even if significant and wide-ranging material has not been examined. For example, in *Dorippe* Weber, 1795, the short-legged species *D. quadridens* (Fabricius, 1793) and *D. sinica* Chen, 1980 (Guinot 2023: figs 10A, B, 12A and 10C, D, respectively) have in both sexes a second ambulatory leg merus that is 4–4.5 times as long as high, whereas the long-legged species *D. tenuipes* Chen, 1980 (Guinot 2023: fig. 9D) has a second ambulatory leg merus almost 7 times as long as high. Sexual dimorphism in the leg length, particularly of the merus, occurs for example in *Philippidorippe philippinensis* Chen, 1986, where the first and second ambulatory legs are proportionally shorter and stouter in females than in males (Guinot 2023: fig. 27A, B). The first and second ambulatory legs may not be sexually dimorphic in size, for example in *Dorippoides facchino* (Herbst, 1785), *D. nudipes* Manning & Holthuis, 1986), and *Paradorippe granulata* (De Haan, 1841) (Guinot 2023: figs 16A–D and 24A, B, respectively).

In recent years, we have assembled a large collection of specimens of *Heikeopsis japonica* from China, Taiwan, Korea and Japan, and it is clear that, whereas the first and second ambulatory legs of the Japanese, Taiwanese and Hong Kong specimens are almost always relatively longer, those from localities north of Shanghai to Qingdao, in the northern half of China, are shorter. The purpose of this article is therefore to investigate 1) whether all *Heikeopsis* from Japan have consistently long and slender first and second ambulatory legs according to De Haan’s figure; 2) whether *Neodorippe* (*Neo-*

dorippe) *japonica* var. *taiwanensis* and/or *H. arachnoides* are valid species; and 3) the identities of the *Heikeopsis* material from Vietnam, China and Korea.

MATERIAL AND METHODS

MORPHOLOGICAL ANALYSES

Terminology essentially follows Holthuis & Manning (1990) and Guinot (2023).

A note must be made here about how Holthuis & Manning (1990) refer to the ambulatory legs, which may be confusing. For this species, when they say “second and third legs slender, long ...”, they are actually referring to the second and third ambulatory legs, i.e., pereopods 2 and 3 (P2 and P3), the short and subchelate fourth and fifth legs of dorippids not being truly ambulatory. This must be kept in mind as we discuss the value of the ambulatory legs in the taxonomy of *Heikeopsis* species below.

In the present paper, we use the term “typical morph” for populations in Japan, Taiwan and southern China, with the adult specimens from this area invariably possessing elongate and slender first and second ambulatory legs. As will be treated later, some specimens from these sites also have relatively shorter legs, but we also refer to them as the “typical morph” for convenience. Adult specimens from northern China and Korea have relatively shorter first and second ambulatory legs, and they are referred to as the “short-legged morph”.

Measurements are provided in millimetres, being taken at its maximum (including rostrum and, posteriorly, rim plus strip), and are reported as carapace length (CL) to width (CW), respectively.

Holthuis & Manning (1990 in key p. 72, table p. 76) measured the ratio length/height of the merus of P3, thus highlighting the slenderness of the leg. It is also interesting to compare the ratio of the length of the merus to length of the carapace, thus highlighting the proportions of the leg (Fig. 15). One of us (P. K. L. Ng) took these measurements on the lectotype and paralectotypes of *Heikeopsis japonica* deposited at RMNH (see Yamaguchi & Baba 1993: 300; Fransen *et al.* 1997: 83) and specimens in the ZRC; T. Naruse did the same on specimens deposited at OMNH and on additional specimens of HMNH and KMNH, and D. Guinot on the rich Japanese collection of *H. japonica* deposited at SMF (see Guinot 2023: 238). Overall, almost 200 specimens were studied.

As many records of *Heikeopsis japonica* in the literature are only in lists and without figures, or only with a few lines of description lacking morphological data, in particular the legs, we will consider that the reports from Japan relate to the true *H. japonica* for the time being, since all the Japanese *Heikeopsis* that we have examined or that are featured in the literature have long, thin ambulatory legs. *Heikeopsis japonica* from Korea is known from numerous lists without figures, but we will rely on the excellent drawing by Kamita (1941a: fig. 4) and the photographs in Ko & Lee (2013: figs 10, 11), as well on the present specimens examined (Figs 6G, H; 14C, D).

ABBREVIATIONS

ICZN *International Code of Zoological Nomenclature.**Institutions*

HMNH Hiwa Museum of Natural History, Hiroshima;
 MNHN Muséum national d'Histoire naturelle, Paris;
 NHM Natural History Museum, previously British Museum (Natural History), London;
 NTOU National Taiwan Ocean University, Keelung City;
 OMNH Osaka Museum of Natural History, Osaka;
 RMNH The Naturalis Biodiversity Centre (ex Rijksmuseum van Natuurlijke Historie), Leiden;
 RUMF Ryukyu University Museum, Fujukan, University of the Ryukyus, Okinawa;
 SMF Senckenberg Research Institute and Natural History Museum, Frankfurt am Main;
 SNUC Seoul National University, Seoul;
 ZLKU Zoological Laboratory, Kyushu University, Fukuoka;
 ZRC Zoological Reference Collection, Lee Kong Chian, Natural History Museum, National University of Singapore.

Material

coll. collected by;
 det. identified by;
 leg. donated by;
 ♀ female;
 ♂ male.

Morphology

CL carapace length;
 CW carapace width;
 G1 male first pleopod;
 G2 male second pleopod;
 P2–P5 pereopods 2–5 (first to fourth ambulatory legs, respectively).

MOLECULAR ANALYSES

DNA was extracted from leg muscular tissue using either a Qiagen Blood and Tissue Kit or a Qiagen BioSprint with the Plant Kit (but lysis with 10ml Qiagen Proteinase K (20mg/ml) added) according to the manufacturer's instructions. Fragments of the mitochondrial 16S rRNA (16S, *c.* 590 bp) and Cytochrome c oxidase subunit 1 gene (COI, *c.* 600 bp) were amplified by polymerase chain reaction (PCR) and sequenced using and respectively primers 16Sa-L and 16Sb-H2 (Palumbi 1996) and LCO1490 and HCO2198 (Folmer *et al.* 1994). Amplifications were conducted in 25 µL volumes containing 50–100 ng DNA, 1× PCR buffer, 200 mM of each dNTP, 0.5 mM of each primer, 2 mM MgCl₂ and 1 U of Taq polymerase. After an initial denaturation step of 3 min at 94°C, 35 cycles of 30 sec at 94°C, 60 sec at 52°C for 16S or 48°C for COI and 60 sec at 72°C were performed, followed by a final extension step of 5 min at 72°C. PCR products were sent to Macrogen Europe for purification and sequencing of both strands of the amplified gene fragments using the primers as given above.

Contigs of forward and reverse strands were assembled using Geneious Prime (v. 2019.2.1) and corrected by eye. Newly produced sequences were aligned with 26 dorippoid sequences retrieved from GenBank produced by Fan *et al.* (2004), Sin *et al.* (2009) and Windsor & Felder (2014) (Table 1) using

Muscle algorithm (Edgar 2004) implemented in MEGA 11 (Tamura *et al.* 2021). To determine the best substitution model for Bayesian inference analyses (see below), hierarchical likelihood ratio tests were carried out with jModelTest 2 (Darriba *et al.* 2012). Based on the Akaike Inference Criterion (AIC), the GTR + G model was retained.

All new sequences (26 sequences of *Heikeopsis* and one sequence of *Nobilum*) have been deposited in GenBank (for accession numbers and museum voucher numbers see Table 1). Phylogenetic trees were reconstructed by Bayesian inference (BI; Huelsenbeck & Ronquist 2001) using MrBayes 3.2.7 (Ronquist & Huelsenbeck 2003) implemented in the Cyber Infrastructure for Phylogenetic Research (CIPRES) portal v. 3.3 (Miller *et al.* 2010: <https://www.phylo.org/>). The MCMC-algorithm was run with four independent chains for 10 000 000 generations, samplefreq = 1000, and burnin = 10%. Maximum likelihood (ML) analyses were run with RaxML-NG (Kozlov *et al.* 2019) and branch support was obtained through non-parametric bootstrapping (1000 replicates; Felsenstein 1985). BI and ML analyses were run using the molecular evolution model specified above.

The dataset was analysed using Assemble Species by Automatic Partitioning (ASAP) (Puillandre *et al.* 2021) to provide statistical support for species hypotheses. This method implements a hierarchical clustering algorithm that uses pairwise genetic distances and proposes species partitions ranked by a new scoring system (the lower the score, the better the partition) that uses no biological prior insight of intraspecific diversity.

SYSTEMATICS

Section EUBRACHYURA Saint Laurent, 1980
 Subsection HETEROTREMATA Guinot, 1977
 Superfamily DORIPPOIDEA H. Milne Edwards, 1837
 Family DORIPPIDAE H. Milne Edwards, 1837
 Subfamily HEIKEOPSINAE Guinot, 2023

Genus *Heikeopsis* Ng, Guinot & Davie, 2008

Heikea Holthuis & Manning, 1990: 71.

Heikeopsis Ng, Guinot & Davie, 2008: 59 (replacement name, name pre-occupied by *Heikea* Isberg, 1934 [Mollusca]). — Guinot 2023: 266, 273.

Heikeopsis japonica (von Siebold, 1824)
 (Figs 1–19)

Dorippe [sic] *Japonica* von Siebold, 1824: 14 (see footnote 5); 1826: 8; 1850: xiii (Shimonoseki or Nagasaki, see below). — Stimpson 1858: 163 (Hakodadi [sic, Hakodate]). — Herklots 1861: 137 (Japan). — Ives 1891: 216 (Japan). — Serène 1937: 77 ('Indochine').

Dorippe callida – De Haan 1839: pl. 31, fig. 1 [Not *Dorippe callida* Fabricius, 1798].

TABLE 1. — Datasets for the genetic samples analysis for the mitochondrial 16S rRNA gene of dorippid species.

Species	Specimen voucher	Locality	GenBank accession number	Reference
<i>Heikeopsis japonica</i>	MBMCAS V310B-6	East China Sea	AY452769	Fan <i>et al.</i> 2004
<i>Heikeopsis japonica</i>	MBMCAS D7B-10	East China Sea	AY452770	Fan <i>et al.</i> 2004
<i>Dorippe tenuipes</i>	MBMCAS Q39B-1	East China Sea	AY452771	Fan <i>et al.</i> 2004
<i>Dorippe tenuipes</i>	MBMCAS K82B-17	East China Sea	AY452772	Fan <i>et al.</i> 2004
<i>Paradorippe granulata</i>	MBMCAS D64B-1	East China Sea	AY452773	Fan <i>et al.</i> 2004
<i>Paradorippe granulata</i>	MBMCAS D64B-1	East China Sea	AY452774	Fan <i>et al.</i> 2004
<i>Neodorippe callida</i>	MBMCAS 00085	East China Sea	AY452775	Fan <i>et al.</i> 2004
<i>Paradorippe polita</i>	MBMCAS C37B-9	East China Sea	AY452776	Fan <i>et al.</i> 2004
<i>Paradorippe polita</i>	MBMCAS C37B-9	East China Sea	AY452777	Fan <i>et al.</i> 2004
<i>Paradorippe granulata</i>	ZRC 1999.0082	Japan	EU636941	Sin <i>et al.</i> 2009
<i>Paradorippe granulata</i>	ZRC 1999.0082	Japan	EU636942	Sin <i>et al.</i> 2009
<i>Neodorippe simplex</i>	ZRC 2003.0335	Australia	EU636943	Sin <i>et al.</i> 2009
<i>Heikeopsis arachnoides</i>	ZRC 1997.392	Taiwan	EU636944	Sin <i>et al.</i> 2009
<i>Philippidorippe philippinensis</i>	ZRC 2008.0075	Philippines	EU636945	Sin <i>et al.</i> 2009
<i>Dorippe quadridens</i>	ZRC 2008.0064	Japan (Okinawa)	EU636946	Sin <i>et al.</i> 2009
<i>Dorippe quadridens</i>	ZRC 2008.0064	Japan (Okinawa)	EU636947	Sin <i>et al.</i> 2009
<i>Dorippe sinica</i>	ZRC 1999.0470	China	EU636948	Sin <i>et al.</i> 2009
<i>Dorippoides nudipes</i>	ZRC 2001.1057	Thailand	EU636949	Sin <i>et al.</i> 2009
<i>Medorippe lanata</i>	ZRC 1999.0632	Israel	EU636950	Sin <i>et al.</i> 2009
<i>Ethusa sexdentata</i>	ZRC 2018.1066	Philippines	EU636951	Sin <i>et al.</i> 2009
<i>Ethusa sexdentata</i>	ZRC 2023.0592	Philippines	EU636952	Sin <i>et al.</i> 2009
<i>Ethusa sexdentata</i>	ZRC uncat.	Philippines	EU636953	Sin <i>et al.</i> 2009
<i>Ethusina macrospina</i>	ZRC 2003.0229	Taiwan	EU636954	Sin <i>et al.</i> 2009
<i>Serpenthusa brucei</i>	ZRC 2008.0025	Vanuatu	EU636955	Sin <i>et al.</i> 2009
<i>Ethusa lata</i>	—	—	KF452987	Windsor & Felder 2014
<i>Ethusa panamensis</i>	—	—	KF453013	Windsor & Felder 2014
<i>Heikeopsis japonica</i>	ZRC 2023.0043	N. China	PQ684417	Present study
<i>Heikeopsis japonica</i>	ZRC 2023.0043	N. China	PQ684418	Present study
<i>Heikeopsis japonica</i>	ZRC 2023.0044	N. China	PQ684419	Present study
<i>Heikeopsis japonica</i>	ZRC 2023.0044	N. China	PQ684420	Present study
<i>Heikeopsis japonica</i>	ZRC 2023.0044	N. China	PQ684421	Present study
<i>Heikeopsis japonica</i>	ZRC 2023.0044	N. China	PQ684422	Present study
<i>Heikeopsis japonica</i>	ZRC 2023.0044	N. China	PQ684423	Present study
<i>Heikeopsis japonica</i>	ZRC 2023.0045	N. China	PQ684424	Present study
<i>Heikeopsis japonica</i>	ZRC 1997.0392	Taiwan	PQ684425	Present study
<i>Heikeopsis japonica</i>	ZRC 1997.0622	Taiwan	PQ684426	Present study
<i>Heikeopsis japonica</i>	ZRC 1998.0330	China	PQ684427	Present study
<i>Heikeopsis japonica</i>	ZRC 1998.0488	China	PQ684428	Present study
<i>Heikeopsis japonica</i>	ZRC 1999.0467	China	PQ684429	Present study
<i>Heikeopsis japonica</i>	ZRC 2004.0636	Taiwan	PQ684430	Present study
<i>Heikeopsis japonica</i>	ZRC 2021.0745	China (Hong Kong)	PQ684431	Present study
<i>Heikeopsis japonica</i>	ZRC 2021.0746	China (Hong Kong)	PQ684432	Present study
<i>Heikeopsis japonica</i>	ZRC 2021.0747	China (Hong Kong)	PQ684433	Present study
<i>Heikeopsis japonica</i>	ZRC 2021.0748	China (Hong Kong)	PQ684434	Present study
<i>Heikeopsis japonica</i>	ZRC 2021.0778	China (Hong Kong)	PQ684435	Present study
<i>Heikeopsis japonica</i>	SNU 271101#006	South Korea	PQ684436	Present study
<i>Heikeopsis japonica</i>	ZRC 1969.5.5.1-2	Japan	PQ684437	Present study
<i>Nobilum histrio</i>	ZRC 1991.0075	Malaysia	PQ684438	Present study
<i>Heikeopsis japonica</i>	SNU 271101#005	South Korea	PQ684439	Present study
<i>Heikeopsis japonica taiwanensis</i>	ZRC 1997.0622 ♂	Taiwan	PQ684440	Present study
<i>Heikeopsis japonica taiwanensis</i>	ZRC 1997.0622 ♀	Taiwan	PQ684441	Present study
<i>Heikeopsis japonica</i>	SMF 57861	Japan (Tanabe, Wakayama)	PQ684442	Present study

Dorippe japonica – De Haan 1841: 122, 227 (Japan). — Nees von Esenbeck 1825: 87 (Shimonoseki). — Nishimura & Suzuki 1971: unnumbered fig in p. 102 (Japan). — Miers 1886: 327, 328 (Japan, near Kobe). — Stebbing 1893: 132, fig. 10 (reproduction of De Haan's figure). — Rathbun 1902: 31 (Japan, Wakanoura, Kii). — Terazaki 1902: 87, unnumbered drawing in p. 87 [Japan and Korea]. — Anonymous 1904: 55, pl. 51, fig. 2 (Japan). — Doflein 1904: 292 (Japan). — Stimpson 1907: 167 (Hakodadi [*sic*, Hakodate]). — Parisi 1914: 302 (Japan). — Ihle 1916: 153, 156 (cit.). — Urita 1918: 161 (Japan: Kagoshima Prefecture; Korea). — Bals 1922: 118. — Maki & Tsuchiya 1923: 126, pl. 14, fig. 2

(‘Formose’, i.e., Taiwan). — Urita 1926: ii, 40 (Japan: off Sibusi, Oshumi, Kagoshima Prefecture; Teuchi, Shimo-koshiki-shima). — Ishikawa Prefecture 1928: 55, pls. 52, 53 (Japan). — Rathbun 1931: 99 [China: Tsimei (= Jimei), Amoy (= Xiamen), Foochow (= Fuzhou)]. — Shen 1931: 101, pl. 6, figs 1, 2 (Shaokiwian District and Honkong); 1932: 11, figs 6, 7a-e (North China Sea: Liaotung Peninsula; Liaotung Bay, Peichihli Bay, Shantung Peninsula); 1937a: 169, 171 (North China); 1937b: 305 (list of species from North China); 1940a: 213 (Hong Kong; Shaokiwian, Cheung Chau); 1948: 105 (China: Shantung Peninsula). — Yokoya 1933: 108, 214 (East of Owashi, east coast of Kii Peninsula). — Kamita 1934: fig. 1 (Ko-

rea); 1935: 62 (Korea); 1936: 30 (Korean Strait); 1941a: 28, figs 5, 6 (Korea); 1941b: 232, table (Korea); 1963: 21 (southern part of Japan Sea: Oki Islands). — Sakai 1934: 283 (Nagasaki); 1936: 41, fig. 5 (Japan); 1937: 72, pl. 10, fig. 1 (Japan: Nagasaki, Onomiti, Yasima, Tosa Bay; Korea: Zinsen); 1940: 49, fig. 3 ('common to Japan, China and Manchoukuo'). — Lin 1949: 12 (Taiwan). — Sakai 1956: 6, 21, fig. 7 (reproduction of De Haan's figure); 1965: 21 (list including Japan, Korea and China). — Kaneko 1958: 332, 336, pl. 15, fig. 10. — Miyake 1961a: 13 (sea around Amakusa); 1961b: 165, 170 (Kyushu: Sea of Ariake). — Miyake *et al.* 1962: 126 (Amakusa). — Chang 1963: 1 (Taiwan). — Shen & Liu 1963: 144 (list, Chinese Seas). — Serène 1968: 40 (cit.). — Holthuis & Sakai 1970: 46, 90, 116, 309, pl. 8, fig. 3 (reproduction of De Haan's fig.). — Kim 1970: 9 (list, Korea). — Miyake & Takeda 1978: 2, 33 (Japan: Amakusa). — S. L. Yang 1986: 152 (China). — Zhou & Sun 1986: 223 (China, coast of Liaoning Province). — Dai *et al.* 1986: 48, fig. 24.1, pl. 5, fig. 6 (China seas).

Dorippe cf. japonica – Kaneko 1958: 331.

'Crabes fort curieux' – Fauvel 1880: 31 (China: Ningbo, Zhejiang Province).

Dorippe sima – Fauvel 1880: 196 (not *Dorippe sima* H. Milne Edwards, 1837) (Wu-sha, island near Zhoushan, Zhoushan Islands).

Dorippe histrio – Rathbun 1931: 99. — Shen 1940b: 70, 76 [Not *Dorippe histrio* Nobilili, 1903] (South China: Yen t'ing, Chuanshih).

Dorippe japonica – Dawydoff 1952: 139 (South China Sea: Paracel Islands).

Neodorippe (Neodorippe) japonica – Serène & Rohmimohtarto 1969: 13, figs 19, 20A, B, pl. 2A, 5C, 6Af (Nhatrang Bay, Vietnam; Nagasaki, Japan). — Kim 1973: 290, 610, figs 85, 87, pl. 76, fig. 57a, b (Korea); 1977: 204 (list, Korea). — Kim *et al.* 1981: 285, 291 (list, Korea). — Kim & Kim 1982: 136, table 1 (Korea Strait, Yellow Sea). — Sakai 1976: 61, pl. 22, fig. 1 (Inland Sea; Saga Prefecture; Shimabara Peninsula). — Yamaguchi *et al.* 1976: 34 (Japan: vicinity of Aitsu Marine Biological Station). — Morita 1977: 16, pl. 2, figs 1-4 (Holocene fossil, Japan: Osaka City). — K. Sakai & Nakano 1983: 81 (Japan: Shikoku Island).

Neodorippe (Neodorippe) japonica var. *taiwanensis* Serène & Romimohtarto, 1969: figs 21, 22, pl. 5A, B, D (Taiwan: Chilung, type locality).

[Japanese name] – Imajima *et al.* 1970: 16, coloured fig. (Japan). — Sakai 1980: 4, fig. 12 (Japan).

Neodorippe japonica – Takeda 1975: 121 (coloured figures); 1982: 93 (coloured figure) (Japan); 1983: 121 (coloured figure) (Japan). — Miyake & Takeda 1978: 33 (Japan); . — Terada 1981: 21-28, 30, 31, figs 1A, 2A, 3A, 4A (zoeae, Japan: east coast of Honshu Island and Enshu Nada, Shizuoka Prefecture). — Sugano 1981: 124-131 (as *Heike-gani*), 186, fig. 39 (Japan). — Horikoshi *et al.* 1982: 126 (Tosa Bay). — Sakai 1985: 330 *pro parte*, figs 1, 3 top, not fig. 3 (Japan and China).

Nobilium (Neodorippe) japonica – C. M. Yang 1979: 3 (cit.).

Nobilium (Neodorippe) japonica var. *taiwanensis* – C. M. Yang 1979: vii, 3 (Taiwan).

Nobilium japonicum taiwanense – Manning & Holthuis 1981: 31 (cit.).

Nobilium japonicum japonicum – Miyake 1983: 17, 198, pl. 6, fig. 1 (Japan). — Muraoka & Konishi 1988: 125 (zoeae).

Nobilium arachnoides Manning & Holthuis, 1986: 364, fig. 1d (Japan: Inland Sea, near Kobe).

Nobilium japonicum – Chen 1986: 123, fig. 5.23-27 (China: 'from the coast of my country').

Nobilium [sic] *japonica* – Yamaguchi *et al.* 1987: 8, pl. 1, fig. 10 (list, photo, Japan: Amakusa Islands).

Heikea japonica – Holthuis & Manning 1990: figs 29 (Jimei, Fukien Province, China), 30 (Japan), 31 (Jimei), 32 (Hong Kong), 33 (Taiwan: holotype of *Neodorippe japonica* var. *taiwanensis*), 34 (reproduction of 1839 De Haan's fig.), 35 (reproduction of 1932 Shen's fig.). — Yamaguchi & Baba 1993: 30 (list), 300, fig. 90-A, 90-B (Japan: list of lectotype and paralectotypes). — Wada 1995: 383, pl. 102-2. — Fransen *et al.* 1997: 83 (list of lectotype and paralectotypes deposited at RMNH). — Ng & Huang 1997: 267, figs 3F, 4B (Taiwan). — Muraoka 1998: 16. — Umemoto & Karasawa 1998: 11, fig. 7; Japan (Holocene fossil, Japan: Aichi Prefecture). — Takeda *et al.* 2000: 139, table 1 (list; possible record from Sagami Bay). — Itani & Fujihara 2001: 47, fig. 1 (carrying behaviour). — Yamaguchi & Holthuis 2001: 30, pl. 5, figs 41, 42 (pictures of *Heikea japonica*). — Chen & Sun 2002: 222, fig. 94 (various parts of China, including Taiwan, Nansha, South China Sea). — Marumura & Kosaka 2003: 23 (Shizuoka, Japan; Taiwan). — Yamaguchi & Baba 2003: 3. — Takeda & Ueshima 2006: 67 (Kyushu, Bingo (eastern Hiroshima), Bicchu (western Okayama), Kii, Sagami Bay, Incheon) [list]. — Takeda *et al.* 2006: 190. — Machida *et al.* 2009: 535, pl. 1B. — Takigawa 2017: 102, fig. 1 (historic study).

Heikea arachnoides – Holthuis & Manning 1990: 72, figs 27, 28 (Japan: Inland Sea, near Kobe and Inland Sea without more details). — Ng & Huang 1997: 267, figs 3E, 4A (Ilan County, northeastern Taiwan). — Takeda *et al.* 2000: 139, table 1 (list). — Chen & Sun 2002: 220, fig. 93, pl. 1-4 (Taiwan).

Dorippe (Neodorippe) japonica – Dai & S. L. Yang 1991: 54, fig. 24.1, pl. 5, fig. 6 (China seas).

Heikea japonicum [sic] – Ng *et al.* 2001: 8 (Taiwan).

Heikeopsis japonica – Ng *et al.* 2008: 59 (list). — Ko & Lee 2013: 19, figs 10, 11 (Korea). — Wang *et al.* 2013a: 513, table 2; 2013b: 1392. — Ng *et al.* 2017: 36, fig. 3a. — Wang *et al.* 2017: Appendix 1. — Takeda *et al.* 2011: 34, figs 5-14 (Japan: around Tottori Prefecture). — Wu *et al.* 2016: Appendix 1 (Japan: Yellow Sea, and China: Bohai). — Davie 2015: fig. 71-2.31.E. — Takeda *et al.* 2019: 13. — Sasaki 2019: 7788 (references). — Luque *et al.* 2021: fig. 5a. — Khim *et al.* 2021: table S2 (Korean Peninsula). — Lee *et al.* 2021: table S2 (Korea).

Heikeopsis japonicus [sic] – Luo *et al.* 2015: table S (Shandong, China).

Heikeopsis arachnoides – Ng *et al.* 2017: 36 (Taiwan).

Heikeopsis japonica and ?*H. japonica* Guinot 2023: 225, 228, 238, 266-274, 323, 355, 356, 360, figs 1, 2A, 19, 31D, 32D, 35E, 38, 39 (revision).

TYPE MATERIAL AND TYPE LOCALITY

The lectotype and paralectotypes of *Heikeopsis japonica* were selected by Yamaguchi & Baba (1993: 300, figs 90-A. a-1, a-2, b, d-f, 90-B, as *Heikea japonica*) from the type series labelled 'Types, Japan, 1823, Leg. P. H. von Siebold', deposited in Leiden (RMNH.CRUS.D.822) (see Fransen *et al.* 1997: 83, as *Heikea japonica*). The lectotype is the male indicated with an arrow by Yamaguchi & Baba (1993: fig. 90-A, a-2). Photo-

graphs of the lectotype and many paralectotypes were kindly made and sent to us by C. H. J. M. Fransen. This material was subsequently re-examined and photographed by P. K. L. Ng.

The type locality of *Heikeopsis japonica* should be Shimonoseki, as the type specimen(s) examined by von Siebold was a part of J. Cock Blomhoff's collection, and von Siebold (1824: 14, footnote 3) noted on the species as "Ex urbe Zimonozeki affertur, fabulâque antiquâ comitata" [= It is brought from the city of Zimonozeki (= Shimonoseki), accompanied by an ancient legend] (see Introduction and also Takigawa 2017). Although the locality mentioned by De Haan (1841: 122, as *D. callida*) is Nagasaki, neither "Zimonozeki" nor "Nagasaki" is present on the labels of the lectotype and paralectotypes (Yamaguchi & Baba 1993: 300, as *Heikea japonica*; Fransen *et al.* 1997: 83, as *Heikea japonica*). Holthuis & Manning (1990: 77) only indicate the following for five syntypes: 'Japan (probably near Nagasaki), 1823, P.F. von Siebold'. It is also possible that the mythology of Heike and *H. japonica* at Shimonoseki was so strong that J. Cock Blomhoff might have believed his *H. japonica* specimen(s) must have come from this location. In any case, as the distance between Shimonoseki and Nagasaki is only some 160 km, populations from the two localities should belong to a same species.

MATERIAL EXAMINED. — **Japan. Shimabara and Ariake Bay, Nagasaki** • 1 ♂ 19.5 × 20.1 mm, 1 ovigerous ♀ 23.7 × 25.7 mm; Tomioka, Shimabara Bay; 29.V.1957; ZLKU 8337-8338 • 1 ♂ 17.5 × 17.7 mm, 3 ♀ 15.7 × 16.3 – 20.2 × 21.4 mm; Aratsu, Ariake Bay; 4.VI.1957; ZLKU 8350-8353 • 1 ♂ 19.5 × 19.5 mm; Miike Bathing Beach, Omuta, Fukuoka, Ariake Bay; coll. T. Watanabe; 6.IV.2004; OMNH Ar 7003 • 1 ♂ 21.3 × 23.7 mm; Ariake Bay, Nagasaki; coll. T. Sakai, 1969; ZRC 1969.5.5.1 • 1 ♀ 19.6 × 20.7 mm; Ariake Bay, Nagasaki, Japan; coll. T. Sakai; 1969; ZRC 1969.5.5.2 • 4 ♂ 6.0 × 5.8 – 25.9 × 26.4 mm, 3 ♀ 17.1 × 17.3 – 21.5 × 22.8 mm; off Rokkaku River, Saga, Ariake Bay; coll. D. Uyeno; 15.VI.2007; RUMF-ZC-7646. **Kumamoto** • 1 ovigerous ♀ 23.9 × 25.3 mm; off Kawaguchi, Kumamoto, Kumamoto; coll. H. Yoshigou; 27.VII.2009; HMNH-C887. **Kanmon Strait** • 1 ♂ 22.6 × 24.0 mm; Mekari Beach, Moji, Fukuoka, opposite Shimonoseki; coll. J. Fujii; X.1954; ZLKU 9425. **Inland Sea: Hiroshima** • 2 ♀ 8.1 × 8.2 mm, 13.3 × 13.5 mm; river mouth of Hongou River, Minamimatsunaga, Fukue, Hiroshima; coll. H. Yoshigou; 21.VII.2018; HMNH-C1434. **Inland Sea: Ehime** • 1 ♀ 17.9 × 18.6 mm; Off Kamo River, Saijo, Ehime; coll. S. Ishida *et al.*; 30.VIII.2011; OMNH Ar 9232 • 1 ♀ 24.9 × 26.8 mm; Hiuchi Nada, Niihama, Ehime, trawling; coll. H. Yamazaki; 12.XII.2015; OMNH Ar 10085. **Inland Sea: Kagawa** • 1 ♂ 20.1 × 21.5 mm; Teshima Island, Tonosho, Kagawa; coll. S. Miyake; 4.VII.1934; ZLKU 8627. **Inland Sea** • 1 ♂ 15.8 × 16.7 mm [holotype of *Nobilum arachnoides* Manning & Holthuis, 1986]; Inland Sea, near Kobe, Japan; 15-91 m; coll. 'Challenger Expedition', 1875; NHM 84.44 • 1 ♂ 12.2 × 12.5 mm; Inland Sea, Japan; 15-92 m; coll. R. Gordon Smith; 1903; NHM 1903.6.7.10 • 1 ♂ 15.2 × 15.7 mm; Inland Sea, Japan; 15-92 m; coll. R. Gordon Smith; 1903; NHM 1903.6.7.5. **Osaka Bay**. 7 ♂ 20.9 × 20.3 – 27.8 × 29.2 mm; 6 ♀ 22.0 × 23.9 – 27.0 × 28.7 mm; off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 23.III.1976; OMNH Ar550-562 • 3 ♂ 23.4 × 24.0 – 24.7 × 24.8 mm, 1 ♀ 24.2 × 26.5 mm; off Misaki, Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar738-741 • 3 ♂ 20.8 × 21.8 – 26.0 × 27.5 mm; 5 km off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar742-744 • 4 ♂ 17.9 × 18.5 – 20.4 × 21.0 mm, 3 ♀ 21.6 × 22.6 –

25.9 × 27.2 mm; off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar746-752 • 3 ♂ 23.3 × 24.1 – 24.8 × 26.0 mm; off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar754-756 • 1 ovigerous ♀ 21.2 × 22.9 mm; off Tanigawa, Tanagawa, Misaki, Sennnan, Osaka Bay; -20 m; coll. Y. Nabeshima; 3.VII.1981; OMNH Ar2551 • 1 ♂ 25.6 × 26.1 mm, 1 ♀ 22.7 × 24.8 mm; N Kansai International Airport; Osaka Bay; 34°29'N, 134°17'30"E; coll. K. Hatooka; 19.IX.1995; OMNH Ar12010 • 1 ♂ 20.8 × 20.9 mm; Osaka Bay; coll. Osaka Prefectural Fisheries Experimental Station; early 1970s; OMNH Ar12349 • 2 ♂ 22.5 × 24.5, 25.6 × 26.6 mm, 1 ♀ 25.2 × 28.4 mm; Osaka Bay; coll. Osaka Prefectural Fisheries Experimental Station; OMNH Ar12350 • 3 ♂ 18.3 × 18.5 – 24.8 × 26.1 mm, 2 ♀ 25.0 × 27.5, 26.0 × 28.4 mm; 5 km off Sennnan, Osaka Bay, coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar12351 • 10 ♂ 19.3 × 20.3 – 24.5 × 25.3 mm; 6 ♀ 23.4 × 25.3 – 28.1 × 30.6 mm; off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar12352 • 4 ♂ 23.5 × 24.7 – 26.4 × 28.0 mm, 9 ovigerous ♀ 19.5 × 20.7 – 26.5 × 28.9; 1-5 km off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 17.VI.1976; OMNH Ar12353 • 10 ♂ 17.1 × 16.8 – 25.7 × 27.2 mm, 13 ♀ 22.0 × 23.8 – 29.3 × 31.8; off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar12354 • 2 ♂ 21.1 × 21.8 – 25.8 × 27.4 mm, 9 ♀ 22.7 × 24.4 – 26.3 × 28.4 mm; 5 km off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar12355 • 4 ♂ 19.5 × 19.7 – 23.9 × 24.5 mm, 2 ♀ 25.0 × 27.1, 27.5 × 30.6 mm; off Sennnan, Osaka Bay; trawling; coll. Osaka Prefectural Fisheries Experimental Station; 24.III.1976; OMNH Ar12356. **Kii Channel** • 5 ♂ 20.4 × 22.6 – 22.0 × 24.3 mm, 2 ovigerous ♀ 24.1 × 27.3, 25.6 × 29.2 mm; off Yoshinogawa, Tokushima, Kii Channel; 34°3.489'N, 134°38.697'E; coll. K. Sakai; no date; SMF 57849 • 15 ♂ 17.0 × 18.5 – 24.2 × 25.6 mm, 8 ovigerous ♀ 22.0 × 25.0 – 25.8 × 28.9 mm; off Okinose, Tsuda-Tokushima, Kii Channel; coll. K. Sakai; 14.II.2002; SMF 57854 • 2 ♂ 19.3 × 20.1, 22.2 × 23.3 mm, 1 ♀ 23.3 × 25.1 mm; off Komatsu Island, Tokushima, Kii Channel; coll. K. Sakai; 9.VII.1991; SMF 57864. **Unknown localities** • Lectotype, ♂ 27.4 × 26.0 mm, paralectotypes, 1 ♂ 14.4 × 14.2 mm, 5 ♀ 17.1 × 18.2, 28.2 × 24.9 mm; coll. von Siebold; RMNH.CRUS.D.822 • paralectotypes, 4 ♂ 13.2 × 13.2 – 18.9 × 20.0 mm, 3 ♀ 16.3 × 17.5 – 18.5 × 19.3 mm; coll. von Siebold; RMNH.CRUS.D.1605 • 1 ♂ 25.0 × 27.3 mm, 1 ♀ 23.5 × 26.7 mm; Chaffanjon; dry condition; MNHN entry 174-1896; E.-L. Bouvier det. 1899 *Dorippe japonica*; MNHN-IU-2000-4091 (= MNHN-B4091) • 1 ♀ 16.8 × 18.6 mm; dry condition; Japan Sea; coll. von Siebold; MNHN-IU-2000-34 (= MNHN-B34). **Korea** • 1 ♂ 15.7 × 16.2 mm; fishery market, Oenardo Port, Jeollanam-do, South Korea; coll. 20.X.2001; SNUC 271101#005 • 1 ♂ 16.9 × 17.1 mm; from net of fishery ship, Saemangeum, Buan-gun, Jeollanam-do, South Korea; coll. 22.VIII.2003; SNUC 271101#006. **Taiwan** • 1 ♂ 21.4 × 22.5 mm; Tahsi, Ilan, northern Taiwan; coll. J. C. Y. Lai & N. K. Ng; 1.XII.2003; ZRC 2004.0636 • 1 ♂ 21.3 × 23.7 mm; Tahsi, Ilan, Taiwan; coll. P. K. L. Ng; 3-4.VIII.1996; ZRC 1997.0392 • 3 ♂ 19.9 × 20.5 – 20.4 × 22.4 mm, 2 ♀ 18.9 × 22.2 – 21.1 × 24.2 mm; Tahsi, Ilan province, northern Taiwan, from fishermen catches; coll. P. K. L. Ng; 3-4.VIII.1996; ZRC 1997.0622 • 1 ♂ 22.0 × 23.2 mm; Toucheng, Ilan Province; northeastern Taiwan, Taiwan; coll. C.-H. Wang; 11.XI.1990; ZRC 1995.0611 • 3 ♂ 17.9 × 18.8 – 23.5 × 25.3 mm, 1 ♀ 21.6 × 24.5 mm; Tashi, Ilan Province, northern Taiwan; coll. K. X. Lee; 2000; ZRC 2001.0013 • 1 ovigerous ♀ 21.2 × 23.9 mm; Nangfangao, Su-Ao, Ilan County, northern Taiwan; coll. P. K. L. Ng; 28.V.1997; ZRC 1998.488 • 3 ♀ 18.6 × 20.5 – 25.2 × 28.1 mm; Tashi port, Ilan Province, northern Taiwan; coll. P. K. L. Ng; 17.XI.1997; ZRC 2021.0727 • 1 juvenile ♂ 9.3 × 9.2 mm, 1 juvenile ♀ 9.5 × 9.0 mm; off Kueshan Island, off Tahsi Port, Ilan Province, northern Taiwan; coll. P. K. L. Ng & P.-H. Ho; 24.V.2024; ZRC 2024.0092.

China. Qingdao and Shandong • 2 ♂ 19.3 × 19.4, 23.9 × 24.6 mm, 2 ovigerous ♀ 25.1 × 27.0 mm, 26.4 × 28.5 mm, 1 ♀ 21.6 × 24.1 mm; Tuandao, Qingdao; from shallow water fishermen nets; coll. P. K. L. Ng; 23-25.VIII.2002; ZRC 2002.0491 • 1 ♂ 19.1 × 18.9 mm; in fishery trawl; Qingdao, Shandong Province, northern China; coll. students; 16.IV.2022 [donated by Li Xinzhen]; ZRC 2023.0043 • 1 ♂ 17.5 × 18.4 mm; same data as for preceding; MNHN-IU-2024-6082 • 1 ♂ 19.8 × 20.2 mm, 1 ovigerous ♀ 20.9 × 22.8 mm, 1 ♀ 21.3 × 22.8 mm; Dingziwan Harbour, Jimo, Qingdao, Shandong Province, northern China; coll. Wen Zou; 16.IV.2022 [donated by Li Xinzhen]; ZRC 2023.0044 • 1 ♂ 22.6 × 23.6 mm, 1 ovigerous ♀ 21.6 × 22.6 mm; same data as for preceding; MNHN-IU-2024-6083 • 1 ♂ 19.7 × 19.9 mm, 1 ovigerous ♀ 22.2 × 24.1 mm; off Qingdao, Tuanda, from inshore fishermen; coll. P. K. L. Ng; 23-25.VIII.2002; ZRC 2002.0491 • 1 ♂ 18.9 × 19.1 mm, 1 ♀ 21.3 × 23.1 mm; Laizhou City, Shandong; coll. Pan Da; VIII.2010; ZRC 2023.0037 • 1 ♂ 29.0 × 30.3 mm, 1 ovigerous ♀ 24.0 × 26.6 mm; North China Sea; 10 m; soft bottom; coll. trawl; 10.V.1959; H. Chen det. 1987; MNHN-IU-2018-5197 (= MNHN-B18801 • 1 ovigerous ♀ 24.3 × 26.7 mm; in fishery trawl, Subei Shoal, Jiangsu Province, northern China; coll. 27.IV.2019; ZRC 2023.0045. **Jiangsu, Shanghai** • 2 ♂ 18.7 × 18.9, 18.8 × 19.0 mm; Qi Dong, Shanghai; coll. Y. Y. Li; 1.V.1996; ZRC 1998.330. **Guangdong and Nanao** • 5 ♂ 12.8 × 13.0 – 22.6 × 23.2 mm, 3 ♀ 21.0 × 20.9 – 26.5 × 28.6 mm; Qianjiang fish port, Nanao County, Guangdong, southern China; coll. Y. Cai & N. K. Ng; 14.XI.1998; ZRC 1999.0469 • 1 ♂ 13.1 × 13.3 mm; Houzhai market, Nanao County, Guangdong; coll. Y. Cai & N. K. Ng; 12.XI.1998 ZRC 1999.0467. **Hong Kong** • 7 ♂ 22.1 × 20.8 mm, 23.8 × 22.6 mm, 3 ♀, station W1; 22°11.259'N, 113°55.232'E – 22°12.285'N, 113°59.086'E; 7.4–19.9 m; coll. K. Wong *et al.*; University of Hong Kong trawls; 30.VII.2018; ZRC 2021.0744 • 1 ♂ 21.3 × 22.0 mm; station E1, northeast of New Territories; 22°26.990'N, 114°16.843'E – 22°29.456'N, 114°24.886'E; 14.8–23.6 m; coll. K. Wong *et al.*; University of Hong Kong trawls; coll. 17.III.2014; ZRC 2021.0745 • 1 ♂ 17.0 × 17.5 mm; station E1, northeast of New Territories; 22°26.990'N, 114°16.843'E – 22°29.456'N, 114°24.886'E; 14.8–23.6 m; coll. K. Wong *et al.*; University of Hong Kong trawls; 10.XI.2018; ZRC 2021.0746 • 1 ♂ 13.6 × 14.3 mm; station S1, southeast of Hong Kong Island; 22°09.967'N, 114°16.442'E – 22°12.951'N, 114°18.552'E; 9.4–34.0 m; coll. K. Wong *et al.*; University of Hong Kong trawls; 14.XI.2012; ZRC 2021.0747 • 1 ♂ 20.3 × 20.6 mm; station SW3, northwest of Lantau Island; 22°14.517'N, 113°50.099'E – 22°17.062'N, 113°52.152'E; 6.2–27.3 m; coll. K. Wong *et al.*; University of Hong Kong trawls; VIII.2007; ZRC 2021.0748 • 1 ♂ 15.8 × 16.4 mm; station W2, southwest of Lantau Island; 22°11.264'N, 113°51.358'E – 22°12.926'N, 113°54.570'E; 4.0–11.6 m; coll. K. Wong *et al.*; University of Hong Kong trawls; 27.VIII.2012; ZRC 2021.0749 • 1 ovigerous ♀ 23.7 × 26.2 mm; station E2; station E2; northeast of New Territories; 22°29.537'N, 114°20.802'E – 22°30.275'N, 114°22.018'E; 7.4–23.0 m; coll. K. Wong *et al.*; University of Hong Kong trawls; 23.VII.2018; ZRC 2021.0777 • 1 ♀ 24.9 × 26.7 mm; station E4; northeast of New Territories, Hong Kong; 22°27.094'N, 114°15.629'E – 22°28.676'N, 114°18.093'E; 9.7–21.8 m; coll. K. Wong *et al.*; University of Hong Kong trawls; 30.VII.2012; ZRC 2021.0778. **Vietnam** • 1 ♂ 18.4 × 19.4 mm; Nhattrang, Vietnam, on muddy bottom; by trawlers; X.1955; ZRC 1969.12.18.1.

DESCRIPTION (MODIFIED FROM HOLTHUIS & MANNING 1990)

Carapace

Carapace 0.89–1.19 times (mean 1.06, $n = 239$) broader than long, convex. Dorsal surface sculptured, with delineated human faces. Frontal region distinctly setose, remainder of carapace much less so. Main grooves very distinct. Mesogastric region low, protogastric region lacking distinct tubercles or oblique

swellings. Urogastric area depressed, with a median tubercle, may be salient or low, or not discernible. Branchial regions swollen, each with oblique dorsal carina. Front consisting of two blunt teeth separated by wide shallow U-shaped emargination. Outer margin of front separated from inner orbital lobe by concavity; inner orbital lobe straight or sinuous. Postorbital fissure closed or narrowly open in some specimens. Outer orbital lobe unarmed, inconspicuous. Exorbital tooth well developed, slender or blunt, falling short of front. Suborbital margin with strong exorbital tooth and short rounded inner orbital tooth, evenly concave, margin granular but unarmed. Antero- and posterolateral margins not demarcated, lacking lateral branchial spine. Carapace posterior rim not extending at all laterally along posterolateral margins and lined posteriorly by narrow strip, thinner medially than laterally, thus slightly concave, in males as in females.

Cephalic structures

Eyes short and stout, widening distally; cornea ventrolateral. Antennule entirely folded into fossa, with basal peduncle more or less long. Antennae: article 2 + 3 quadrate, hardly moveable; article 4 short, bent outwards; article 5 only slightly longer than preceding, bent outwards; both articles 4 and 5 widened and lying nearly horizontally on eyestalk; flagellum long.

Oxystomatous disposition

Openings of exhalant channels scarcely visible in dorsal view.

Chelipeds, P1

Chelipeds equal in size and shape in young males and females but right chela greatly inflated in adult males at variable sizes, with variously shaped and oriented swelling; chela may be inflated in males as small as CL 19.5 mm, usually inflated in males larger than CL 22 mm; inflated chelae usually lacking row of long setae dorsally and ventrally on palm and fingers; surface of palm smooth, even. Fingers of swollen male chela about 1.5 times as long as upper margin of palm; in females and young males fingers about 3 times length of palm; cutting edges of fingers with 9–12 equal teeth, smaller, blunter and fewer on inflated chela of large males. (See VARIATIONS, below).

Ambulatory legs, P2–P5

P2 and P3 (the longest) varying from long, slender, with both reaching beyond front with distal end of merus, to shorter and stouter (Figs 3–5); without spines or with distinct, sometimes sharp granulation, with scattered short setae on surface; merus of P3 varying from 3.72–7.67 times (mean 5.76, $n = 195$) as long as high; dactyli of P2 and P3 as long as or slightly longer than their respective propodi; most of dorsal margin and at least half of ventral margin of dactyli fringed with setae. Propodi strongly flattened, not conspicuously carinate, but with shallow longitudinal groove on upper (posterior) and lower surfaces. Carpus with indistinct dorsal fringe of setae, shorter than propodus and almost half as long as merus. P5 merus slightly beyond base of merus of P3 and overreaching base of merus of P4.

Thoracic sternum

Thoracic sternum of male rather wide. Sternite 1 usually with small portion dorsally visible. Sternite 2 salient, with distinct straight external margins, and forming a quadrangular piece; sternite 3 oval and laterally extended, consisting of smooth coalesced median and submedian elevations, and salient curved margins; sternite 4 with median elevation; sternite 5 with marked longitudinal ridges; sternite 6 inflated, with two strong oblique ridges posteriorly; sternite 7 exposed, as long, oblique plate along each side of pleon. Sutures 4/5-7/8 interrupted medially; suture 3/4 only visible laterally, deep and often ending in closed boutonniere ('boutonniere' in French) marked by a perforation; sutures 4/5 and 5/6 with short interruption points; suture 5/6 slightly curved backwards; suture 6/7 interrupted in males, but each end linked by low bridge; suture 5/6 interrupted in females, with each end linked by sulcus, sometimes membranous. Female thoracic sternum progressively tilted backwards at level of weak ridge of sternite 6. In females, fused portion of sternite 8 with erect axial spine, usually very salient but may be low, rarely absent.

Pleon and telson

Male pleon with somites 1, 2 and part of 3 dorsal; female pleon with somites 1-3 and part of 4 dorsally exposed. All somites free. Male pleon more or less constricted at level of pleonal somite 5 and overhung by raised borders of sternopleonal cavity. Telson varying from triangular and slightly elongated to more flattened, with hat-shaped or rounded apex. Tip of telson not very far from suture 4/5. Female pleon smooth, with no sharp teeth or spines, each somite with median prominence; somites 3-5 crossed by marked smooth carina. (See VARIATIONS, below).

Pleonal locking mechanism by press-button

Locking buttons on posterior margins of sternite 5, often as spines. Sockets on pleonal somite 6 very deep and extending on most of length of somite; may be swollen and marked externally. Also effective in females, with locking prominences lying very close to vulvae.

Additional female pleonal-retention mechanism.

In females, strong retention by wide process of sternite 8 overhanging pleonal somite 2.

Male gonopore and penis

Male gonopore coxal. Coxo-sternal condition of penis, the most elaborate of all dorippids and similar to that of ethusids. Sternites 7 and sternite 8 close to one another for long distance (much longer than in any other dorippid), so penis very long, with elongated bulb prolonging into penis without clear demarcation, then long exposed inclined portion and shorter vertical portion covered by well-developed G1 protopodite; bulb and proximal inclined portion of penis clearly visible dorsally between sternite 7 and widely exposed sternite 8. (See VARIATIONS, below).

Gonopods

G1 without basal lobe; inverted C-shaped (in situ), stout proximally; its distal part slender and elongated, strongly bent and largely curved outward; apex elaborate and ending in two elongate, blunt-topped unequal lobes plus two subdistal processes (Vehof 2020: fig. 11A, C, D).

G2 with strongly bent apex (Vehof 2020: fig. 11B). (See VARIATIONS, below).

Vulvae

Vulva at internal part of conspicuous sternal prominence close to sternal bulge of sternite 6, showing as long, extremely narrow, curved, vertically oriented slits, overhung by prominence; opening obliquely directed on submedian area of sternite 6.

Female reproductive system

Two ovaries and two seminal receptacles that open through the vagina and vulva onto thoracic sternite 6. These two sperm storage chambers (e.g., a single sperm storage organ on each side of the body) with a direct connection to the oviducts resembling the condition in other Eubrachyura, as does internal fertilisation (Vehof 2020: 52, figs 4, 5A 6, 22; Guinot 2023: figs 35, 37).

COLOUR IN LIFE

In life, the typical morph is brown to dark brown on all its dorsal aspects, with the ambulatory dactyli maroon, with the adult male chelae cream coloured to white (Fig. 1C, D). The short-legged morph is similarly coloured but generally lighter brown (Fig. 2A-D, G, H), and in one specimen, the overall colour is just pale cream to dirty white (Fig. 2E, F).

VARIATIONS

Measurements of a large number of adult male and female specimens from Japan showed that the CW and CL are highly correlated, with females possessing a slightly wider carapace (Fig. 9) (cf. males: Figs 7A-F, H-L; 8A-E, H, I versus females: Figs 7G; 8F, G).

Adult males sometimes have distinctly asymmetrical chelipeds, with one of the chelae (usually the right) distinctly inflated (Fig. 11). In larger adult male specimens, the right chela is swollen and fully grown at CL 23.4 mm and CW 23.9 mm (with one exception), a size range which is slightly larger than those from northern China (fully grown at CL 21.9 mm and CW 24.0 mm, ZRC 2002.0491, Qingdao; and CL 18.0 mm, CW 19.5 mm, cf. Shen, 1932) (Figs 10; 11). This suggests that Japanese individuals may grow larger than northern Chinese individuals, which may affect comparison of their carapace proportions as well.

There are no obvious differences when large numbers of adult G1 and G2 structures from all the areas are compared. Ng & Huang (1997) had alluded that the distal folds of *H. japonica* and *H. arachnoides* differed slightly but noted that this was based on only a few specimens. The present study shows that the variation in the degree of curvature and structure of the distal folds varies too substantially to see any pattern between populations from Japan, Taiwan,

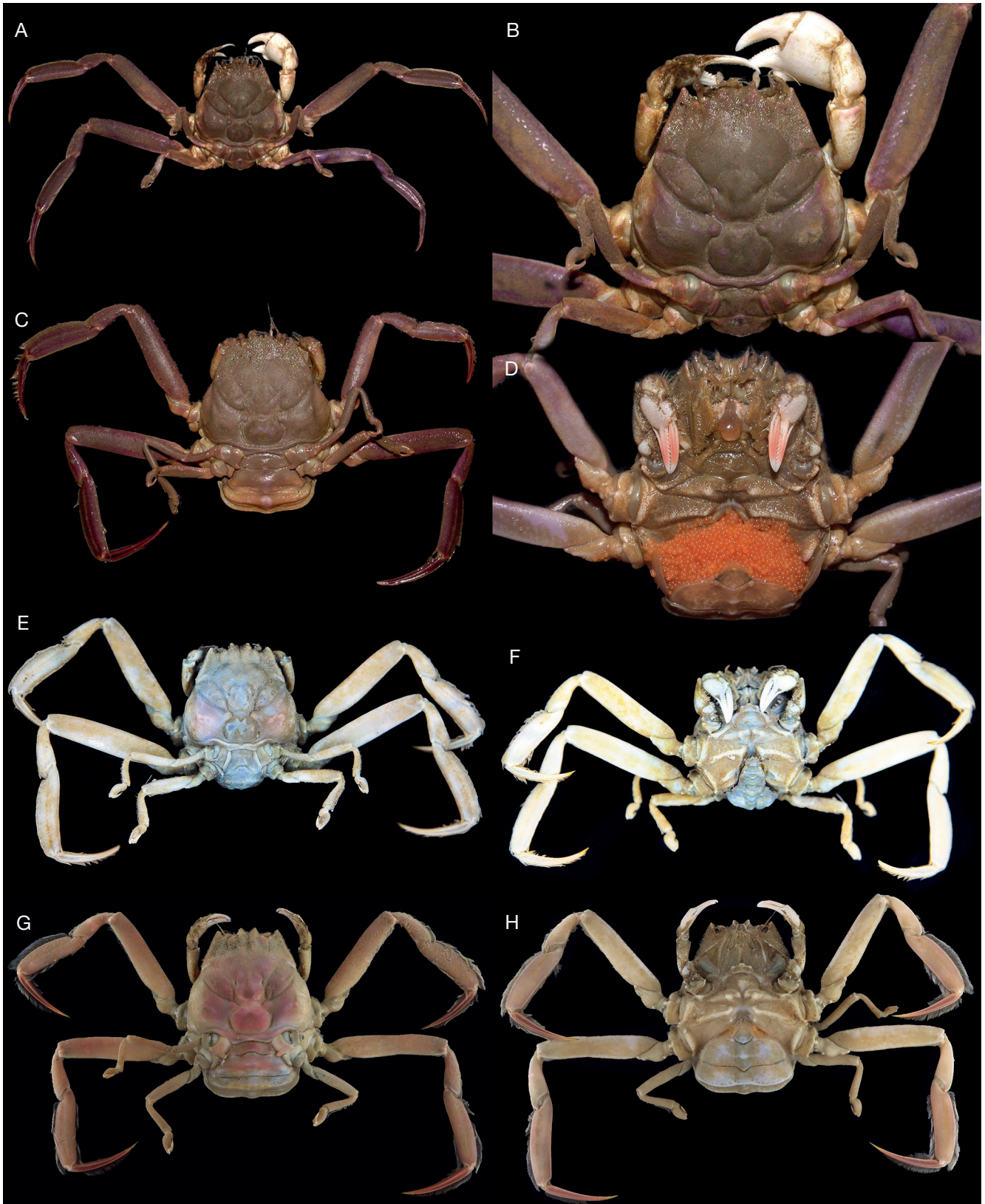


FIG. 2. — *Heikeopsis japonica* (von Siebold, 1824), short-legged morph, colour in life: **A, B**, ♂ 21.9×24.0 mm, Qingdao, northern China, ZRC 2002.491; **C, D**, ovigerous ♀ 22.2×24.1 mm, ZRC 2002.0491, Qingdao, northern China; **E, F**, ♂ 19.8×20.2 mm, ZRC 2023.0044, Qingdao, northern China; **G, H**, ovigerous ♀ 20.9×22.8 mm, Qingdao, northern China, ZRC 2023.0044. **A, C, E, G**, overall dorsal habitus; **B**, carapace; **D, F, H**, ventral surface of cephalothorax. E-H, photograph courtesy of X.Z. Li.



FIG. 3. — *Heikeopsis japonica* (von Siebold, 1824), typical morph, overall dorsal habitus: **A**, lectotype ♂ 26.0×27.4 mm, Japan, RMNH.CRUST.D.822; **B**, ♀ 16.8×18.6 mm, Japan, MNHN-IU-2000-34; **C**, ♀ 23.5×26.7 mm, Japan, MNHN-IU-2000-4091; **D**, ♂ 22.6×24.0 mm, Kyushu, Japan, ZLKU 9425); **E**, ♂ 25.0×27.3 mm, Japan, MNHN-IU-2000-4091; **F**, ♂ 21.3×23.7 mm, Nagasaki, Japan, ZRC 1969.5.5.1; **G**, ♂ 24.2×25.6 mm Tokushima, Japan, SMF 57854; **H**, ♂ 15.2×15.7 mm, Inland Sea, Japan, NHM 1903.6.7.5; **I**, ♂ 12.2×12.5 mm, Inland Sea, Japan, NHM 1903.6.7.10; **J**, ♂ 16.4×16.9 mm (holotype male of *Nobilum arachnoides* Manning & Holthuis, 1986), Inland Sea, Japan, NHM 84.44.



FIG. 4. — *Heikeopsis japonica* (von Siebold, 1824), typical morph, overall dorsal habitus: **A**, ♂ 15.8 × 16.6 mm (holotype of *Neodorippe (Neodorippe) japonica* var. *taiwanensis* Serène & Romimohtarto, 1969), Taiwan, ZRC 1969.2.24.7; **B**, ♀ 15.8 × 17.0 mm (paratype of *Neodorippe (Neodorippe) japonica* var. *taiwanensis* Serène & Romimohtarto, 1969, Taiwan, ZRC 1969.2.24.8; **C**, ♂ 20.4 × 22.1 mm, Taiwan, ZRC 1997.622; **D**, ♀ 21.1 × 24.2 mm, Taiwan, ZRC 1997.0622; **E**, ♂ 21.3 × 23.7 mm, Taiwan; ZRC 1997.0392; **F**, ♂ 22.0 × 23.2 mm, Taiwan, ZRC 1995.0611; **G**, ♂ 25.3 × 23.5 mm, Taiwan, ZRC 2001.13; **H**, ♂ 21.4 × 22.5 mm, Taiwan, ZRC 2004.0636; **I**, ♂ 20.3 × 20.9 mm, Guangdong, southern China, ZRC 1999.0469; **J**, ♂ 13.1 × 13.3 mm, Guangdong, southern China, ZRC 1999.0467.



FIG. 5. — *Heikeopsis japonica* (von Siebold, 1824), typical morph, overall dorsal habitus: **A**, ♂ 21.3 × 22.0 mm, Hong Kong, southern China, ZRC 2021.745; **B**, ♂ 17.0 × 17.5 mm, Hong Kong, southern China, ZRC 2021.746; **C**, ♂ 20.8 × 22.1 mm, Hong Kong, southern China, ZRC 2021.744; **D**, ♂ 22.6 × 23.8 mm, Hong Kong, southern China, ZRC 2021.744; **E**, 20.3 × 20.6 mm, Hong Kong, southern China, ZRC 2021.748; **F**, ♂ 18.4 × 19.4 mm, Vietnam, ZRC 1969.12.18.1.

southern China and Vietnam (Figs 18; 19A–G) and those from northern China (and Korea) (Fig. 19H–Q). The male specimen from Nagasaki (ZRC 1969.5.5.1) is relatively large and, with a CW of 23.7 mm, it is similar in size to most other specimens from Japan and Taiwan. Its pleon, however, is relatively narrower longitudinally overall; pleonal somite 1 is distinctly narrower, somite 6 is relatively more elongated (Fig. 16C, D) and is similar to that of smaller subadult males (e.g., Fig. 16O, P). In addition, its G1 does not appear to be fully developed (Fig. 18A–D), is distinctly shorter, somewhat soft and not well chitinised, and more closely resembles the condition in subadult or juvenile specimens from other locations (e.g., Fig. 18Q–S). In male specimens of similar CW (or smaller), the G1 is already fully developed, being distinctly longer and the distal folds more prominently formed (e.g., Fig. 19H–J, O–Q). The G1 of the type of *Neodorippe* (*Neodorippe*) *japonica* var. *taiwanensis* is unusual and we are not

sure if it is similar to the situation for the Nagasaki male as the flaps, while long, are very flattened, appearing collapsed (Fig. 18I–K); we believe it may be due to the fact that the specimen was preserved before it had fully hardened after molting. The second author has observed the same situation with several specimens of *Paradorippe australiensis* (Miers, 1884) from the Arafura Sea in the Bogor Museum, where male specimens comparable in size to adult specimens have a poorly chitinised and short G1 with the distal parts poorly developed (unpublished information).

DISTRIBUTION

Heikeopsis japonica has a very wide distribution from Kyushu and western Honshu, Japan, Korea, Taiwan, northeastern to southern coast of China to Vietnam (Sakai 1976; Kim 1973; Shen 1931, 1932; Serène & Romimohtarto 1969; Chen & Sun 2002; Takeda *et al.* 2011; Ng *et al.* 2017). Holthuis &



FIG. 6. — *Heikeopsis japonica* (von Siebold, 1824), short-legged morph, overall dorsal habitus: **A**, ♂ 21.9×24.0 mm, Qingdao, northern China, ZRC 2002.0491; **B**, ♀ 23.4×26.4 mm, Qingdao, northern China, ZRC 2002.0491; **C**, ♂ 18.8×19.0 mm, Shanghai, northern China, ZRC 1998.330; **D**, ♂ 18.7×18.9 mm, Shanghai, northern China, ZRC 1998.0330; **E**, ♂ 29.3×31 mm, northern China, MNHN-IU-2018-5197; **F**, ♀ 24.0×26.6 mm, northern China, MNHN-IU-2018-5197; **G**, ♂ 15.7×16.2 mm, Korea, SNUC 271101#005; **H**, ♂ 16.9×17.1 mm, Korea, SNUC 271101#006.

Manning (1990: 82) wrote: “From this, and in the absence of subsequent substantiated records, we assume the following record to be erroneous: Hakodate (Stimpson, 1858, 1907). We are unable to place the record by Parisi (1914) of Kujiukuri, Hitachi, reported by Balss as Kujinkuri (Hitachi); if this is Hitachi, at 36°35'N, 140°40'E, on the east coast of Honshu Island, the record certainly is erroneous. Parisi's locality may

be in Suruga Bay; we are unable to locate any records from that bay in the literature and Sakai specifically questioned a record from there”. This may be a consequence of Sakai's (1976: 62) comment that “The localities formerly recorded for this species, such as Hakodate, Sagami Bay and Suruga Bay are due to error.” Takeda & Ueshima (2006), however, recorded *H. japonica* from Sagami Bay, although the Hako-

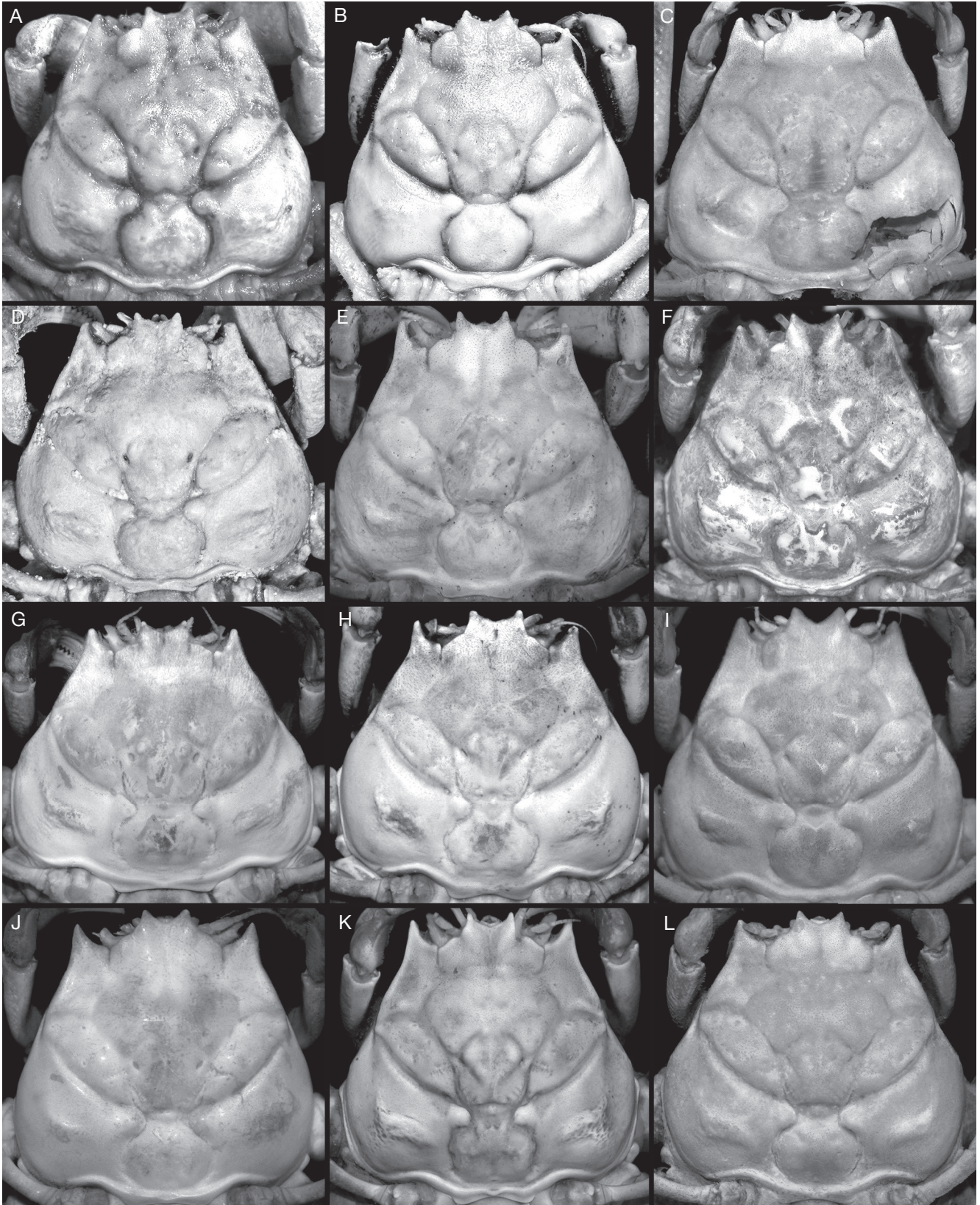


FIG. 7. — *Heikeopsis japonica* (von Siebold, 1824), typical morph, carapace: **A**, lectotype ♂ 26.0 × 27.4 mm, Japan, RMNH D-822; **B**, ♂ 15.8 × 16.7 mm (holotype ♂ of *Nobilum arachnoides* Manning & Holthuis, 1986); Inland Sea, Japan, NHM 84.44; **C**, ♂ 21.3 × 23.7 mm, Nagasaki, Japan, ZRC 1969.5.5.1; **D**, ♂ 25.0 × 27.0 mm, Japan, MNHN-IU-2000-4091; **E**, ♂ 15.8 × 16.6 mm (holotype of *Neodorippe (Neodorippe) japonica* var. *taiwanensis* Serène & Romimoharto, 1969), Taiwan, ZRC 1969.2.24.7; **F**, ♂ 23.5 × 25.3 mm, Taiwan, ZRC 2001.13; **G**, ♀ 21.6 × 23.1 mm, Taiwan, ZRC 2001.13; **H**, ♂ 21.4 × 22.5 mm, Taiwan, ZRC 2004.636; **I**, ♂ 20.3 × 20.9 mm, Guangdong, China, ZRC 1999.469; **J**, ♂ 13.1 × 13.3 mm, Guangdong, China, ZRC 1999.467; **K**, ♂ 21.3 × 22.0 mm, Hong Kong, southern China, ZRC 2021.745; **L**, ♂ 18.4 × 19.4 mm, Vietnam, ZRC 1969.12.18.1.

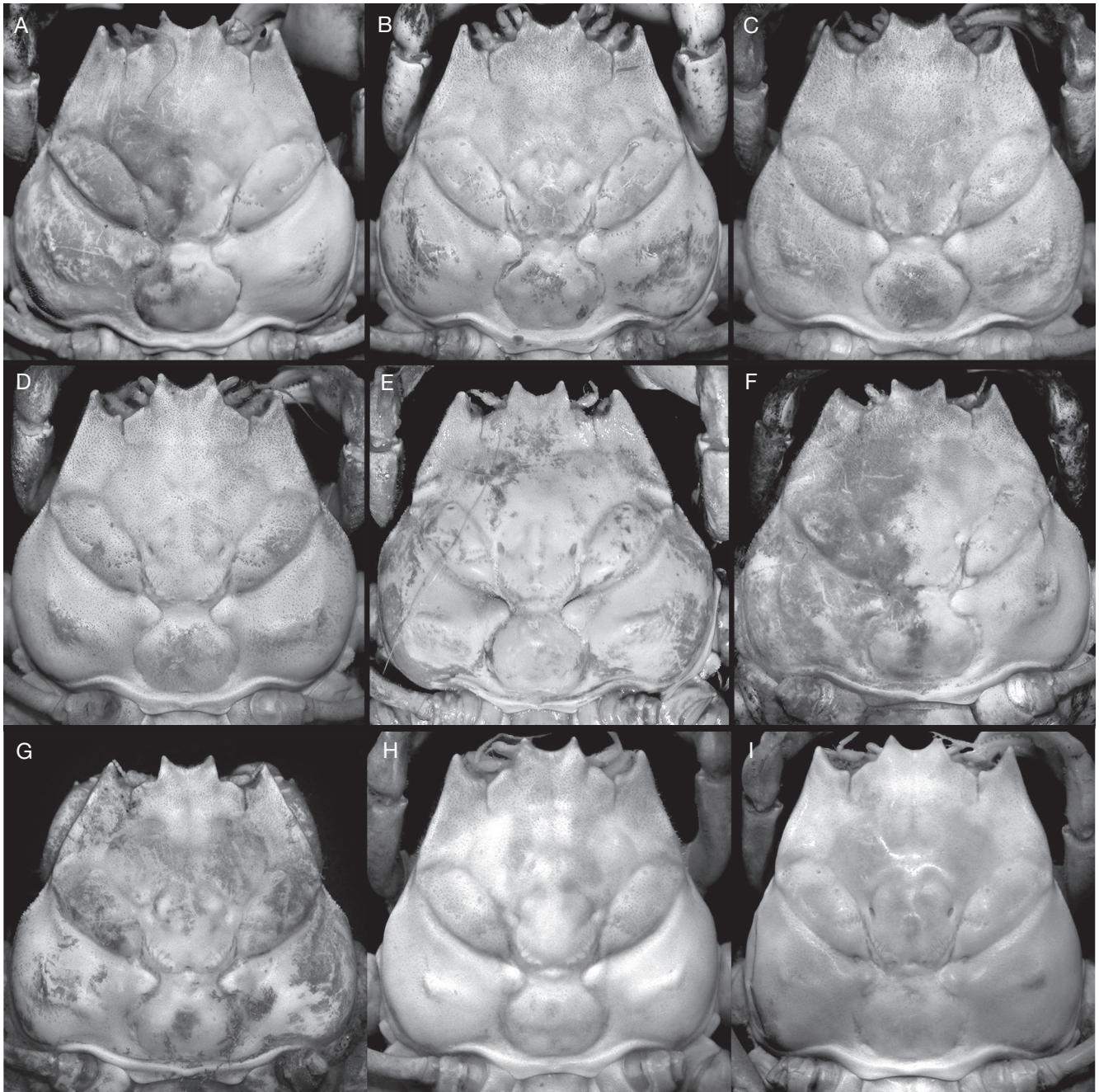


FIG. 8. — *Heikeopsis japonica* (von Siebold, 1824), shorter-legged morph, carapace: **A**, ♂ 21.9×24.0 mm, Qingdao, northern China, ZRC 2002.491; **B**, ♂ 19.3×19.4 mm, Qingdao, northern China, ZRC 2002.491; **C**, ♂ 18.8×19.0 mm, Shanghai, northern China, ZRC 1998.330; **D**, ♂ 18.7×18.9 mm, Shanghai, northern China, ZRC 1998.330; **E**, ♂ 29.3×31 mm, northern China MNHN-IU-2018-5197; **F**, ♀ 23.4×26.4 mm, Qingdao, northern China, ZRC 2002.491; **G**, ovigerous ♀ 24.3×26.7 mm, Jiangsu Province, northern China, ZRC 2023.0045; **H**, ♂ 15.7×16.2 mm, Korea, SNUC 271101#005; **I**, ♂ 16.9×17.1 mm, Korea, SNUC 271101#006.

date record by Stimpson is possibly doubtful as the record was based only on a dredged chela. That being said, it seems entirely possible that *H. japonica* can occur in the south of Hokkaido island in northern Japan, and in any case, Hitachi is just off the east coast of Honshu.

REMARKS

As discussed above, the Japanese, Taiwanese and southern Chinese specimens of *Heikeopsis japonica* that we have examined and are depicted in the literature all have consistently longer

and more slender P2 and P3, in contrast to the northern Chinese specimens with the same specific name, which have proportionately shorter and wider P2 and P3. This poses a problem as to whether the northern Chinese specimens belong to a separate taxon.

Before we can deal with this, we have to discuss the status of two other taxa:

1) *Neodorippe* (*Neodorippe*) *japonica* var. *taiwanensis* Serène & Rohmimohtarto, 1969. It was considered a junior subjective synonym of *H. japonica* by Holthuis & Manning (1990) who

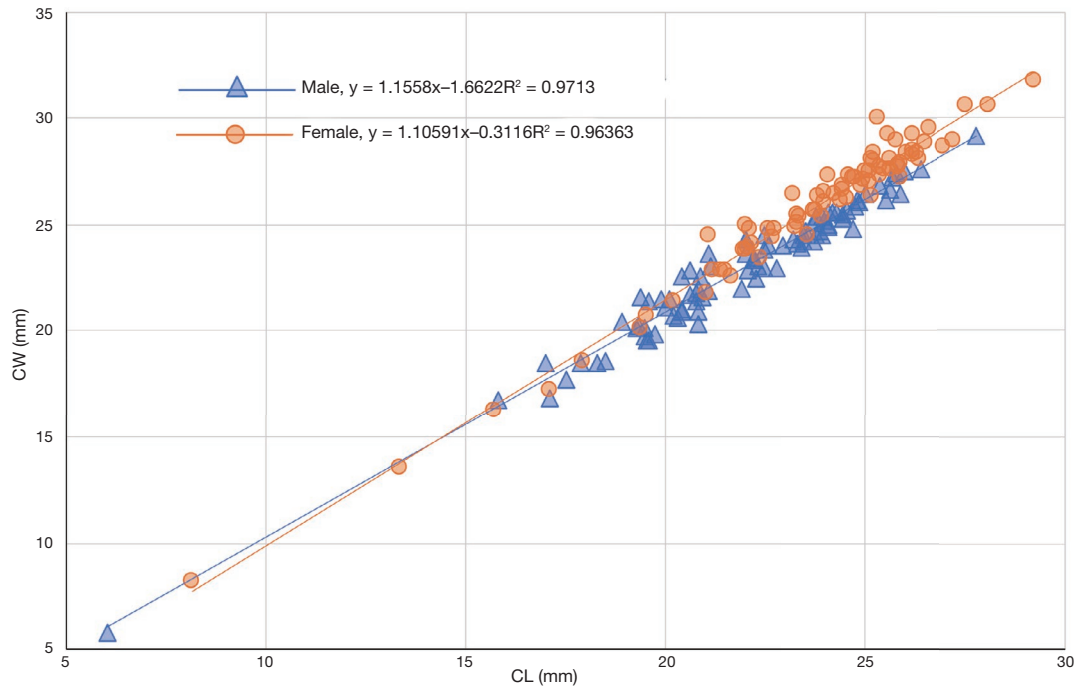


FIG. 9. — Carapace proportions between sexes of *Heikeopsis japonica* (von Siebold, 1824). Females have slightly wider carapaces. Carapace width (**CW**) is highly correlated with carapace length (**CL**) in Japanese population.

had also studied the types. We examined the holotype male (15.8 × 16.6 mm, ZRC 1969.2.24.7) and a female paratype (15.8 × 17.0 mm, ZRC 1069.22.4.8) from Keelung, Taiwan, and they agree very well with the specimens from Japan, as well as extensive material we have from various parts of Taiwan. The G1 of the holotype male has the subdorsal flap relatively short and positioned subparallel to the distal part (Fig. 18I-K), in contrast to those of other specimens in which the dorsal flap is longer and positioned obliquely (e.g., Fig. 18M-O), but this is due to the poor condition of the specimen: the holotype male appears to have freshly moulted when it was caught and preserved, and this easily explains the condition of the G1 (see also Fig. 18A-D and observation for G1 of Nagasaki specimen of *H. japonica* above). As such, we are confident they are synonymous.

2) *Nobilum arachnoides* Manning & Holthuis, 1986. The species was briefly diagnosed and figured by Manning & Holthuis (1986) but the taxonomy was elaborated on by Holthuis & Manning (1990) who referred it to *Heikea*. As discussed earlier, *H. arachnoides* was only separated from *H. japonica* by the relatively longer and more slender P2 and P3 (P3 merus less than 6.3 times longer than height for *H. japonica*; P3 merus of 6.6 to 7.3 times longer than height for *H. arachnoides*). *Heikeopsis arachnoides* was originally established for a single male specimen (the holotype) measuring 15.8 × 16.7 mm with both chelae equal in size (Holthuis & Manning 1990: 73, fig. 27e; thus not a fully adult specimen) from Japan, Inland Sea, near Kobe, dredged at 15–91 m by the HMS ‘Challenger’ in 1875 (NHM 84. 44) (Manning & Holthuis 1986: 364). This specimen had been reported as ‘*Dorippe japonica*’ by Miers (1886: 327). Holthuis & Man-

ning (1990: 72) subsequently included two male specimens collected by R. Gordon Smith in the same Inland Sea area, between 15 and 92 m (NHM 1903.6.7.5, NHM 1903.6.7.10) and listed them as paratypes. This subsequent designation of these two specimens as paratypes is not admissible under the ICZN rules, and they cannot be treated as such (Guinot 2023: 240). Examination of the three specimens (one holotype and two topotypes, not paratypes) by Holthuis & Manning (1990, as *Heikea arachnoides*) show that, while the P2 and P3 are more elongate (P3 merus is about 7.0 times longer than broad) (Fig. 3H-J) than typical material of *H. japonica* from Japan, the difference is not significant. Holthuis & Manning (1990: 73) also noted that the “Second and third legs [...] each reaching beyond front with about half of merus”, but the photograph of the holotype has the proximal half of the P2 and P3 meri not reaching the level of the front when stretched anteriorly. We have a good series of specimens from OMNH that were collected from near the type locality of *H. arachnoides* (within c. 30 km), and the proportions vary, with the length to width ratio ranging from 5.04 to 6.95 (mean 5.97, n = 72) in P3 and 4.42 to 6.35 (mean 5.40, n = 76) in P2 (Figs 12; 13; 15). Ng & Huang (1997: 267, figs 3F, 4B) reported *H. japonica* from Taiwan, but they also noted there was one male specimen (21.3 × 23.7 mm, ZRC 1997.0392) that had relatively longer P2 and P3 and as such, they referred it to *H. arachnoides* (Ng & Huang 1997: 267, figs 3E, 4A). Ng & Huang (1997) commented that the two species were very similar and observed that the G1 of *H. arachnoides* had the distal flap slightly longer than the subdistal process compared to *H. japonica*.

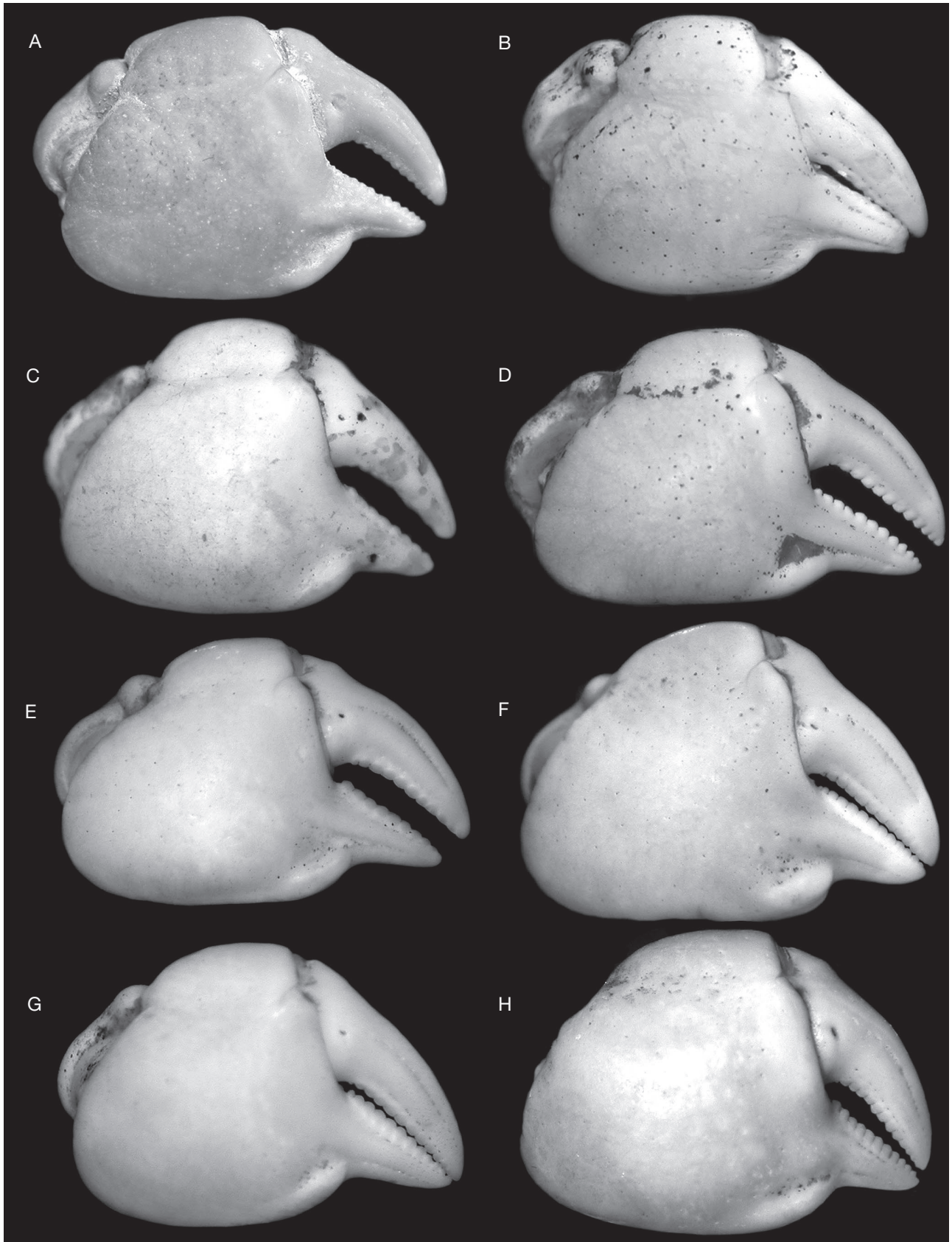


FIG. 10. — *Heikeopsis japonica* (von Siebold, 1824), major σ chela: **A-E**, typical morph; **F-H**, short-legged morph: **A**, lectotype 26.0 × 27.4 mm, Japan, RMNH. CRUST.D.822; **B**, σ 15.8 × 16.6 mm (holotype of *Neodorippe (Neodorippe) japonica* var. *taiwanensis* Serène & Romimohtarto, 1969), Taiwan, ZRC 1969.2.24.7; **C**, σ 20.4 × 22.1 mm, Taiwan, ZRC 1997.622; **D**, σ 22.0 × 23.2 mm, Taiwan, ZRC 1995.611; **E**, σ 23.5 × 25.3 mm, Taiwan, ZRC 2001.13; **F**, σ 21.9 × 24.0 mm, Qingdao, northern China, ZRC 2002.491; **G**, σ 19.3 × 19.4 mm, Qingdao, northern China ZRC 2002.491; **H**, σ 29.3 × 31 mm, northern China, MNHN-IU-2018-5197.

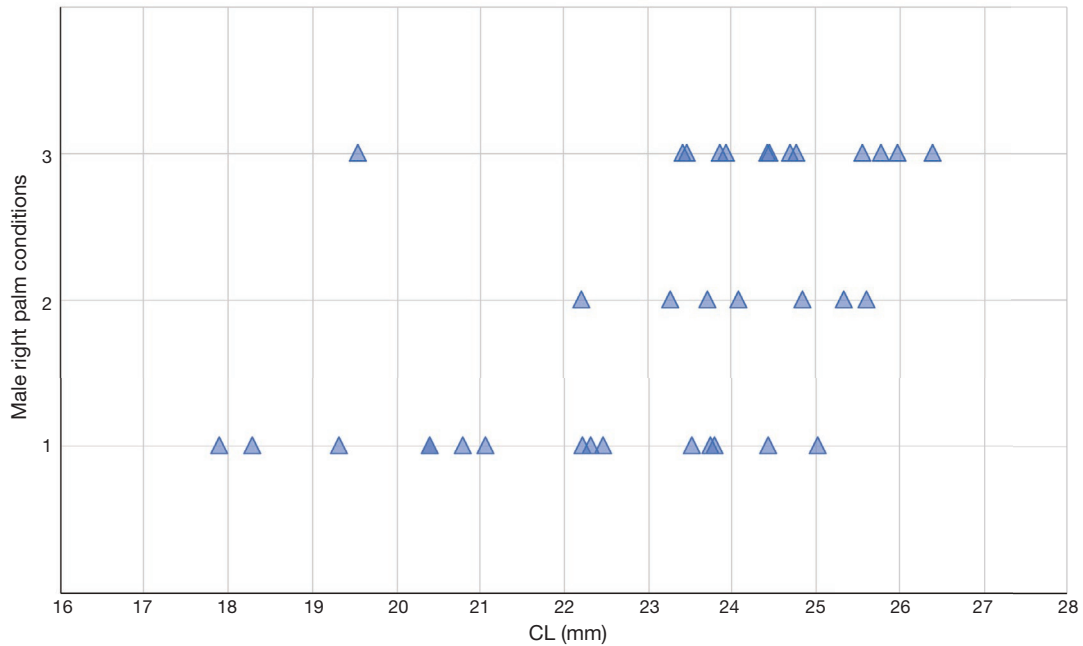


FIG. 11. — Male chelal asymmetry in the Japanese population of *Heikeopsis japonica* (von Siebold, 1824). Male right palm condition is separated into three groups as in the graph below. 1, right palm symmetrical with left palm; 2, right palm not fully grown and larger than left palm; 3, right palm fully grown and distinctly larger than left palm. The male right palm becomes fully-grown around CL 23.4 mm CW 23.9 mm (with an exception), which is slightly larger than northern Chinese population (fully grown in 21.9 × 24.0 mm (Qingdao, ZRC 2002.0491) and 18.0 × 19.5 mm (Shen, 1932)). This may suggest that Japanese individuals grow larger than northern Chinese individuals, which may affect comparison of their carapace proportions.

Chen & Sun (2002: figs 94, 93, respectively) also recognised two species, *Heikea japonica* and *H. arachnoides*, distinguishing them by the length of their legs. Their prognosis was based on the same male specimen (21.3 × 23.7 mm, ZRC 1997.0392) from Taiwan reported by Ng & Huang (1997), compared to 59 males and 40 females of Chinese *H. japonica*; Chen & Sun (2002) did not have any other material of *H. arachnoides*.

Wong *et al.* (2021) recently reported both taxa in Hong Kong: *Heikeopsis arachnoides* along Tolo Channel and *H. japonica* in more western waters, noting that the two species differed in the length of their ambulatory legs: *H. arachnoides* with longer meri, notably P3 meri 6.6 to 7.3 times longer than high; and *H. japonica* with shorter P3 meri, less than 6.3 times longer than high (Wong *et al.* 2021: 10, fig. 11, pl. 2E and fig. 12, pl. 2F, respectively). We have examined their material, and we are of the opinion both are conspecific. The specimens with proportionately longer P2 and P3 are invariably smaller in carapace size (21.3 × 22.0 mm) (Figs 13A-C; 15) while those that are larger (carapace size 23.7 × 26.2 mm) have relatively shorter legs (Figs 12; 13D-F; 15). There are no other notable morphological differences.

While we believe that some Japanese specimens with more slender and elongate P2 and P3 represent the extreme end of the observed variation for *H. japonica* (especially smaller specimens and juveniles) (e.g., Fig. 13A-C), we have found many individuals which have lost their legs in the OMNH material. This is not expected if the specimens had been trawled and fixed in formalin with other catches. We do not know how dorippids regenerate lost legs, but in examination of a large number of individuals we have found neither bud-like regenerating legs

(as seen in grapsoids, for example) nor distinctly shorter legs on the other side. Some asymmetry has been observed, but differences are always subtle (a few millimetres at most). In all the material studied, we found a few cases of leg asymmetry, but we do not know what to attribute them to.

The study of the large series of specimens of *Heikeopsis japonica* from throughout Japan, Taiwan, southern China, Hong Kong and Vietnam shows that they are all the same taxon. The proportions of the legs of these specimens varies from 4.42 to 6.35 (mean 5.40, n = 76) in P2 and from 5.04 to 6.95 (mean 5.97, n = 72) in P3 (Fig. 15), with smaller specimens often possessing a relatively longer P2 and P3. But there are also some larger adult specimens with slightly longer legs (e.g., from Taiwan, 21.3 × 23.7 mm, ZRC 1997.0392) (Figs 4E; 15). It is important to note that the three male specimens (including the holotype) studied by Holthuis & Manning (1990) of an intermediate size, being adult but not fully mature, have the male chelae slender and still not inflated (Fig. 3H-J).

Holthuis & Manning (1990: 74) suggested that *H. arachnoides* may prefer deeper waters the original specimens having been collected between 15 and 92 m, and suggested some older records may be this species, e.g., those by Yokoya (1933) and Horikoshi *et al.* (1982: 126, as Tosa Bay) from east of Owashi, on the east coast of Kii Peninsula, at 132 m, and Sakai (1937) from Korea at 130 m. In any case, in view of the present synonymy of *H. arachnoides* with *H. japonica*, this point is moot. There is also the issue of whether some of the old records, e.g., Sakai's (1937) specimen from Korea may be the short-legged form (see discussion later).



FIG. 12. — *Heikeopsis japonica* (von Siebold, 1824), typical morph, P2-P5: **A**, lectotype ♂ 26.0×27.4 mm, Japan, RMNH.CRUST.D.822; **B**, ♂ 21.3×23.7 mm, Nagasaki, ZRC 1969.5.5.1; **C**, ♂ 15.8×16.6 mm (holotype of *Neodorippe (Neodorippe) japonica* var. *taiwanensis* Serène & Romimohtarto, 1969), Taiwan, ZRC 1969.2.24.7; **D**, 21.4×22.5 mm, Taiwan, ZRC 2004.636; **E**, ♂ 21.3×23.7 mm, Taiwan, ZRC 1997.392; **F**, ♂ 18.4×19.4 mm, Vietnam ZRC 1969.12.18.1. [Legs of each species shot to the same magnification].

We must now address the question of the short-legged *Heikeopsis* from North China. The first probable mention of “*Heikeopsis japonica*” from China may be Fauvel (1880) who, in ‘Promenades d’un naturaliste’ on an island (Ningbo) of the Zhoushan Archipelago (also written as Chusan, which today includes many islands in the Ningbo area of northern China), described a ‘very curious crab’ with a carapace length measuring approximately 3 cm, and with P2 and P3 measuring respectively 6 and 7 cm in total length, i.e., in the case of P2, twice the length of the carapace.

As has been discussed earlier, the distribution of the short-legged and typical more long-legged morphs of *Heikeopsis japonica* in China is compounded by the fact that both are present there, and is complicated by the fact that all adults from northern China are of the former type (Fig. 15). The majority of the Japanese, Taiwanese and southern Chinese (including Hong Kong) are the typical long-legged *H. japonica* (Figs 3; 4A-C, E, G-J; 5A, B, E, F; 12A, C-F; 13A-C, F) with only a few with relatively shorter legs (Figs 4D, F; 5C, D; 12B; 13D, E), and there a few specimens with

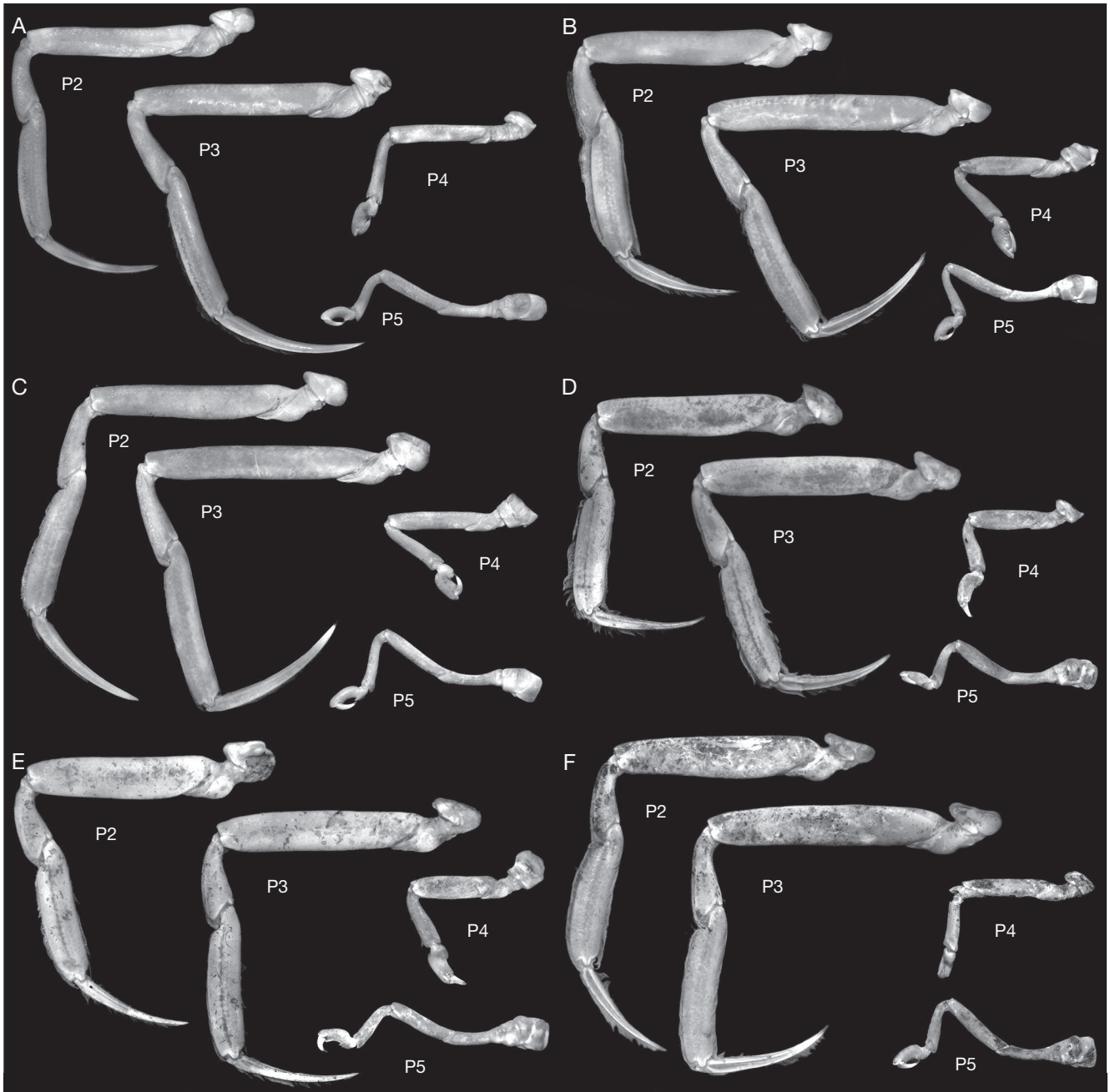


FIG. 13. — *Heikeopsis japonica* (von Siebold, 1824), typical morph, P2-P5: **A**, ♂ 13.1 × 13.3 mm, Guangdong, ZRC 1999.0467; **B**, ♂ 21.3 × 22.0 mm, Hong Kong, southern China, ZRC 2021.745 (laterally inverted); **C**, ♂ 17.0 × 17.5 mm, Hong Kong, southern China, ZRC 2021.0746 (laterally inverted); **D**, ♂ 20.8 × 22.1 mm, Hong Kong, southern China, ZRC 2021.0744; **E**, ♂ 22.6 × 23.8 mm, Hong Kong, southern China, ZRC 2021.744; **F**, ♂ 20.3 × 20.6 mm, Hong Kong, southern China, ZRC 2021.0748. [Legs of each species shot to the same magnification].

intermediate proportions (e.g., Figs 12D; 13F). Adults from northern China (north of Shanghai to Qingdao) on the other hand are all belonging to the short-legged morph (Figs 6; 14A-D). The specimen of *H. japonica* figured by Shen (1931: 101, pl. 6, figs 1, 2) from Hong Kong has relatively longer P2 and P3, and so they belong to the typical long-legged morph of *H. japonica* as now understood, and we have specimens to confirm this. The specimens of *H. japonica* from North China (Shen 1932: 11, figs 6, 7a-e), on the other hand, have clearly shorter P2 and P3 meri, and

belong to the short-legged morph. Chinese records without figures by Shen (1937a: 169, 171; 1937b: 305; 1948: 105) from North China are likely the short-legged morph, while those by Shen (1940a: 213) from Hong Kong and by Shen (1940b: 70, 76 (as *Dorippe histrio*) from South China belong to typical *H. japonica*.

Dai *et al.* (1986), Dai & S. L. Yang (1991: pl. 5, fig. 6) and Chen & Sun (2002) had material from throughout China. This is also true for Japan as Sakai (1937, 1976) who included Korean material as well in their interpretation

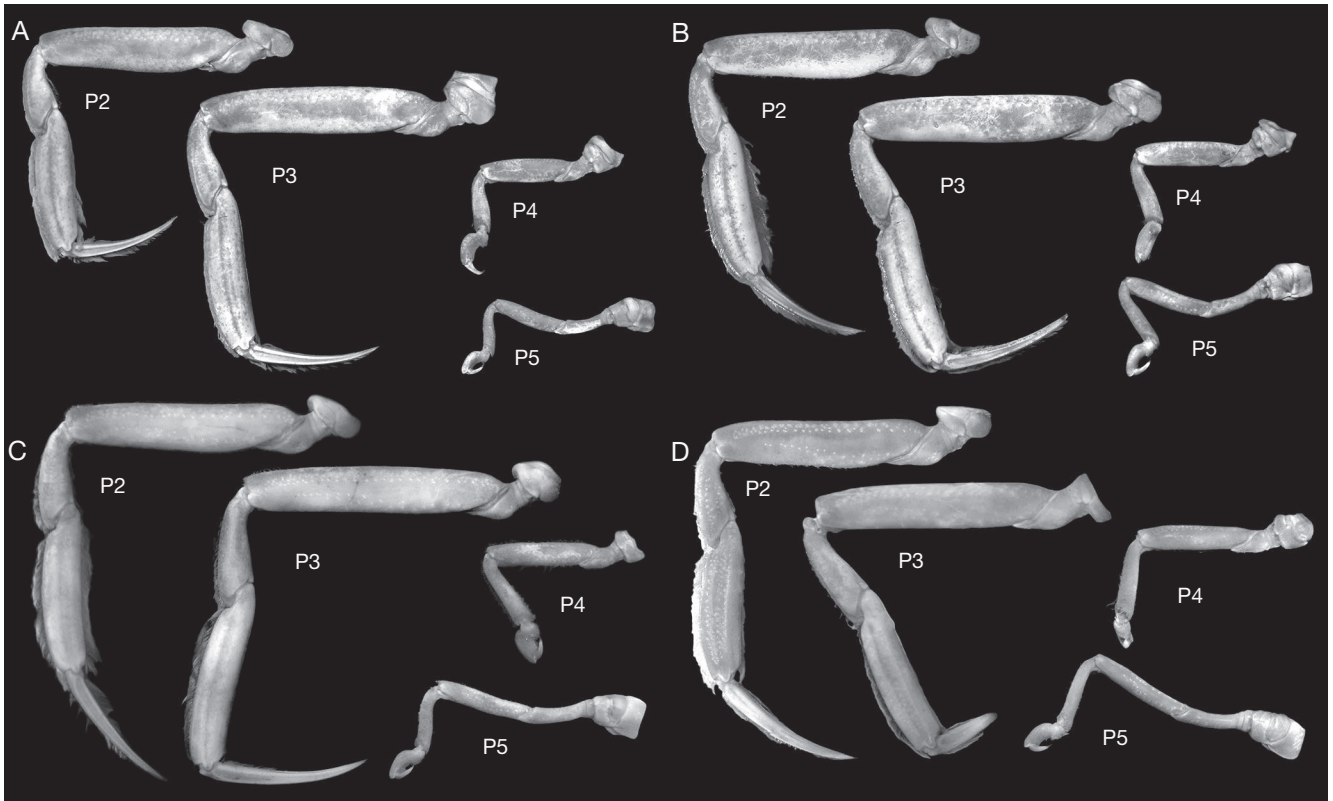


FIG. 14. — *Heikeopsis japonica* (von Siebold, 1824), short-legged morph, P2-P5: **A**, ♂ 21.9 × 24.0 mm, Qingdao, northern China, ZRC 2002.0491; **B**, ♂ 19.3 × 19.4 mm, Qingdao, northern China, ZRC 2002.0491; **C**, ♂ 15.7 × 16.2 mm, Korea, SNUC 271101#005; **D**, ♂ 16.9 × 17.1 mm, Korea SNUC 271101#006. [P2 and P3 for **C**; P4 and P5 for **D**, laterally transposed]. [Legs of each species shot to the same magnification].

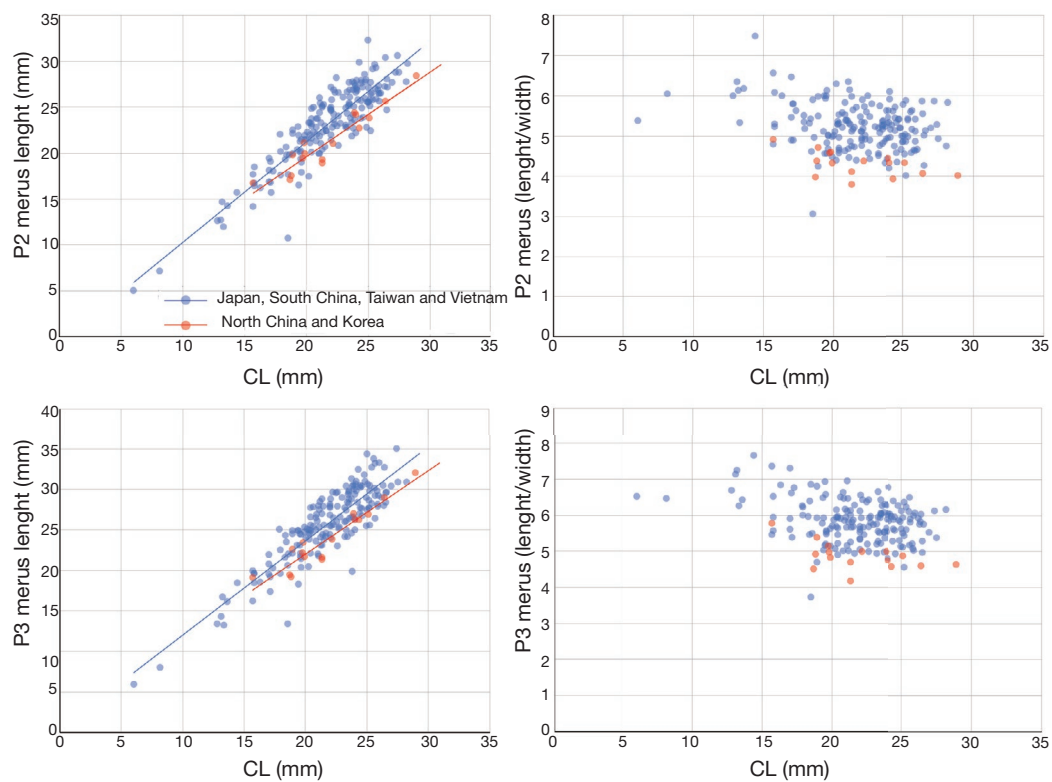


FIG. 15. — *Heikeopsis japonica* (von Siebold, 1824): relationships between P2 and P3 meri length and length to width ratios against carapace length.

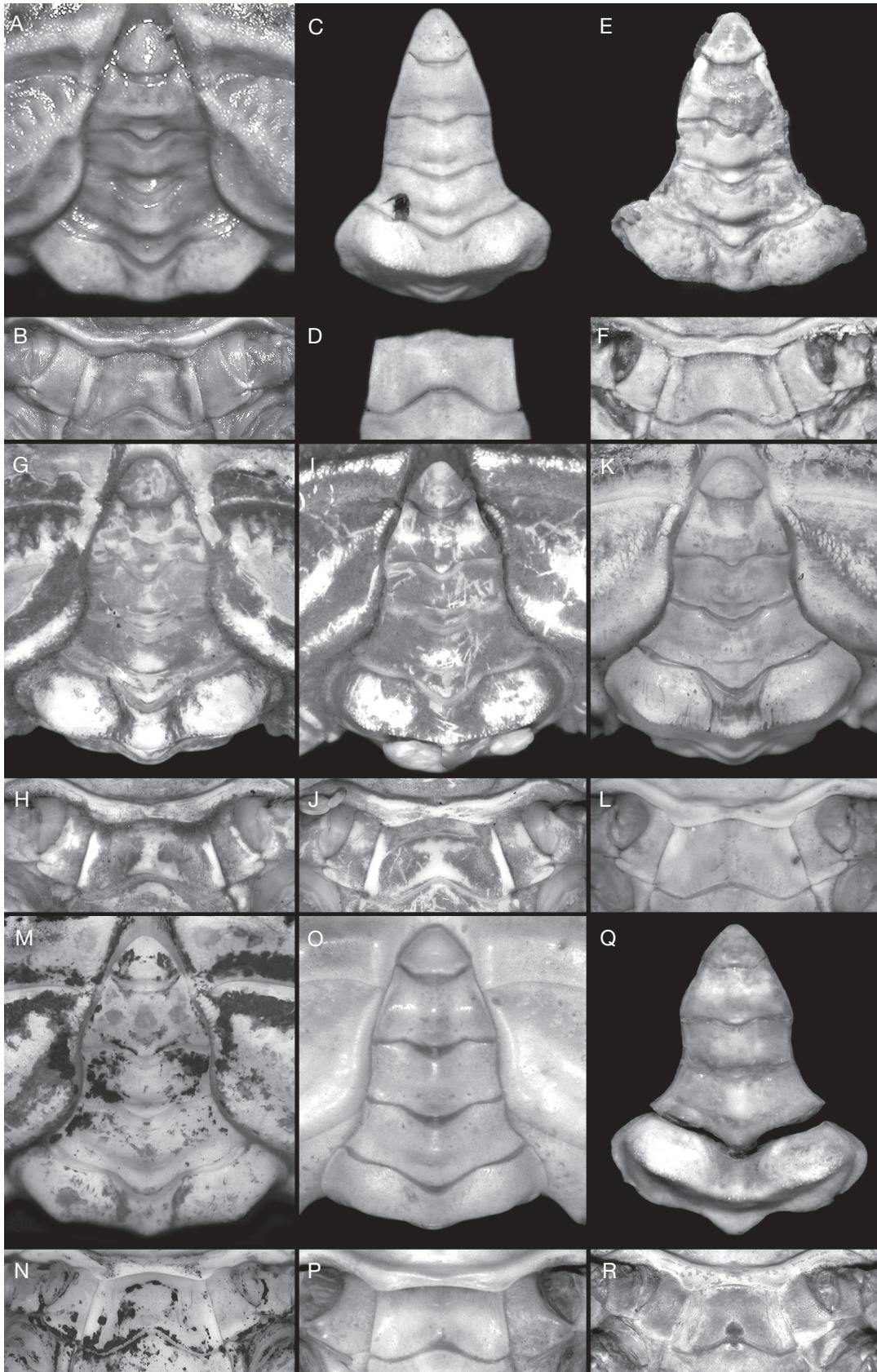


FIG. 16. — *Heikeopsis japonica* (von Siebold, 1824), typical morph, male pleon: **A, B**, lectotype ♂ 26.0×27.4 mm, Japan, RMNH.CRUST.D.822; **C, D**, ♂ 21.3×23.7 mm, Nagasaki, ZRC 1969.5.5.1; **E, F**, ♂ 25.0×27.3 mm, Japan, MNHN-IU-2000-4091; **G, H**, ♂ 23.5×25.3 mm, Taiwan, ZRC 2001.13; **I, J**, ♂ 21.3×23.7 mm, Taiwan, ZRC 1997.392; **K, L**, ♂ 21.4×22.5 mm, Taiwan, ZRC 2004.636; **M, N**, ♂ 20.4×22.1 mm, Taiwan, ZRC 1997.622; **O, P**, ♂ 13.1×13.3 mm, Guangdong, China, ZRC 1999.467; **Q, R**, ♂ 18.4×19.4 mm, Vietnam, ZRC 1969.12.18.1. Male pleonal somites 3-6 and telson (**A, C, E, G, I, K, M, O, Q**); pleonal somite 1 (**B, D, E, H, J, L, N, P, R**).

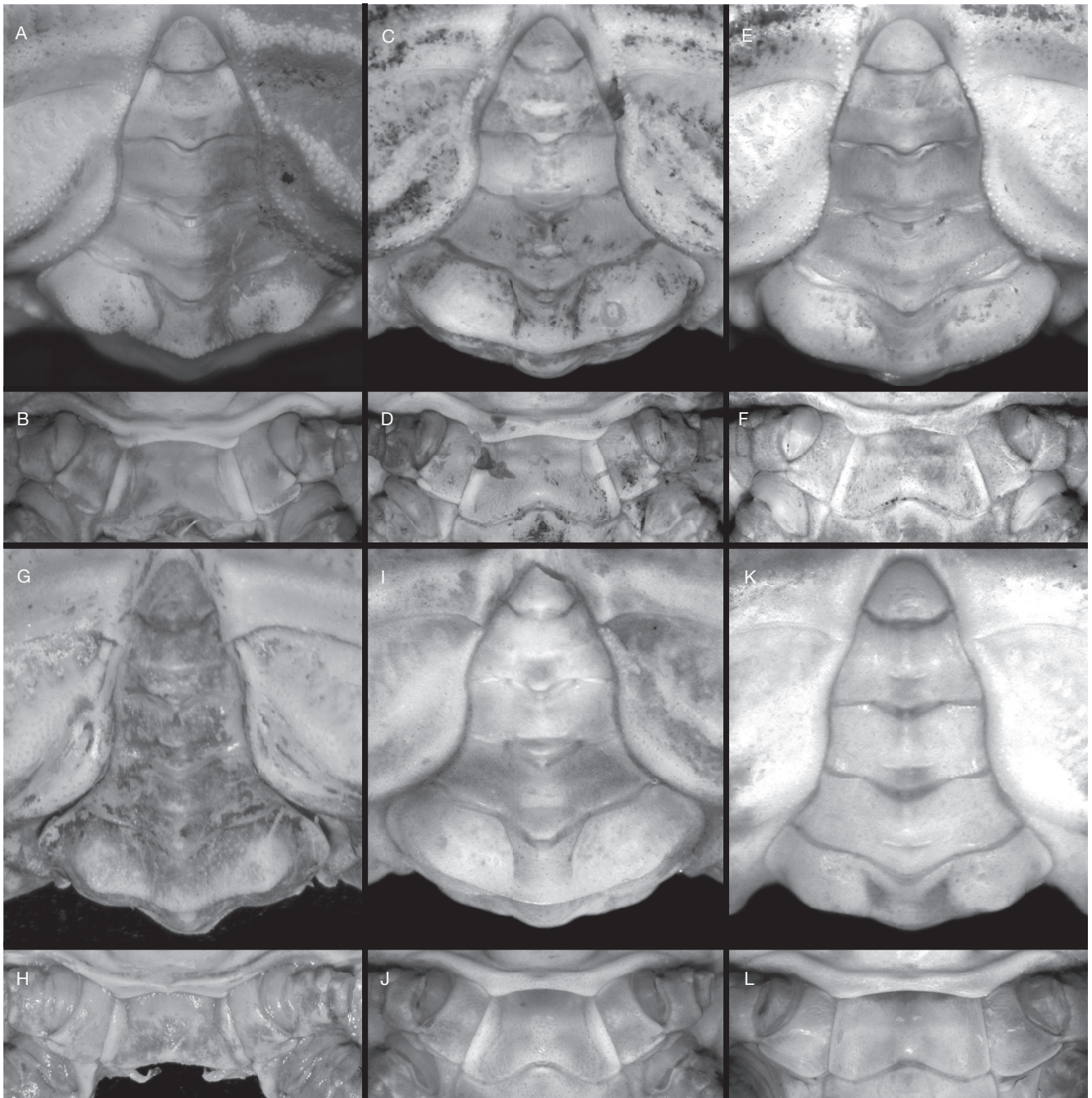


Fig. 17. — *Heikeopsis japonica* (von Siebold, 1824), short-legged morph, male pleon: **A, B**, ♂ 21.9 × 24.0 mm, Qingdao, northern China, ZRC 2002.491; **C, D**, ♂ 19.3 × 19.4 mm, Qingdao, northern China, ZRC 2002.491; **E, F**, ♂ 18.8 × 19.0 mm, Shanghai, northern China, ZRC 1998.330; **G, H**, ♂ 29.0 × 30.3 mm, northern China, MNHN-IU-2018-5197; **I, J**, ♂ 15.7 × 16.2 mm, Korea SNUC 271101#005; **K, L**, ♂ 16.9 × 17.1 mm, Korea, SNUC 271101#006. **A, C, E, G, I, K**, male pleonal somites 3-6 and telson; **B, D, E, H, J, L**, pleonal somite 1.

of the species (see later). The same is true for Holthuis & Manning's (1990) records of *Heikeopsis japonica* as they included in this species short- and long-legged morphs from Japan and China. Chen (1986: 123, fig. 5.23-27, as *Nobilum japonicum*) reported 65 males and 54 females of the species noting (in Chinese) that it inhabits Chinese seas, on substrates of mud and sand from the intertidal zone to depths of 130 m; her figures do not depict the ambulatory

legs, so we do not know their condition. Dai & S. L. Yang (1991: pl. 5, fig. 6) depict a *H. japonica* from China seas with very long and thin legs, but they did not specify where it was from.

On the basis of the geography and the specimens we have examined, we can be fairly certain that Fauvel's (1880) crab from near Ningbo in northern China is the short-legged morph of *H. japonica*.

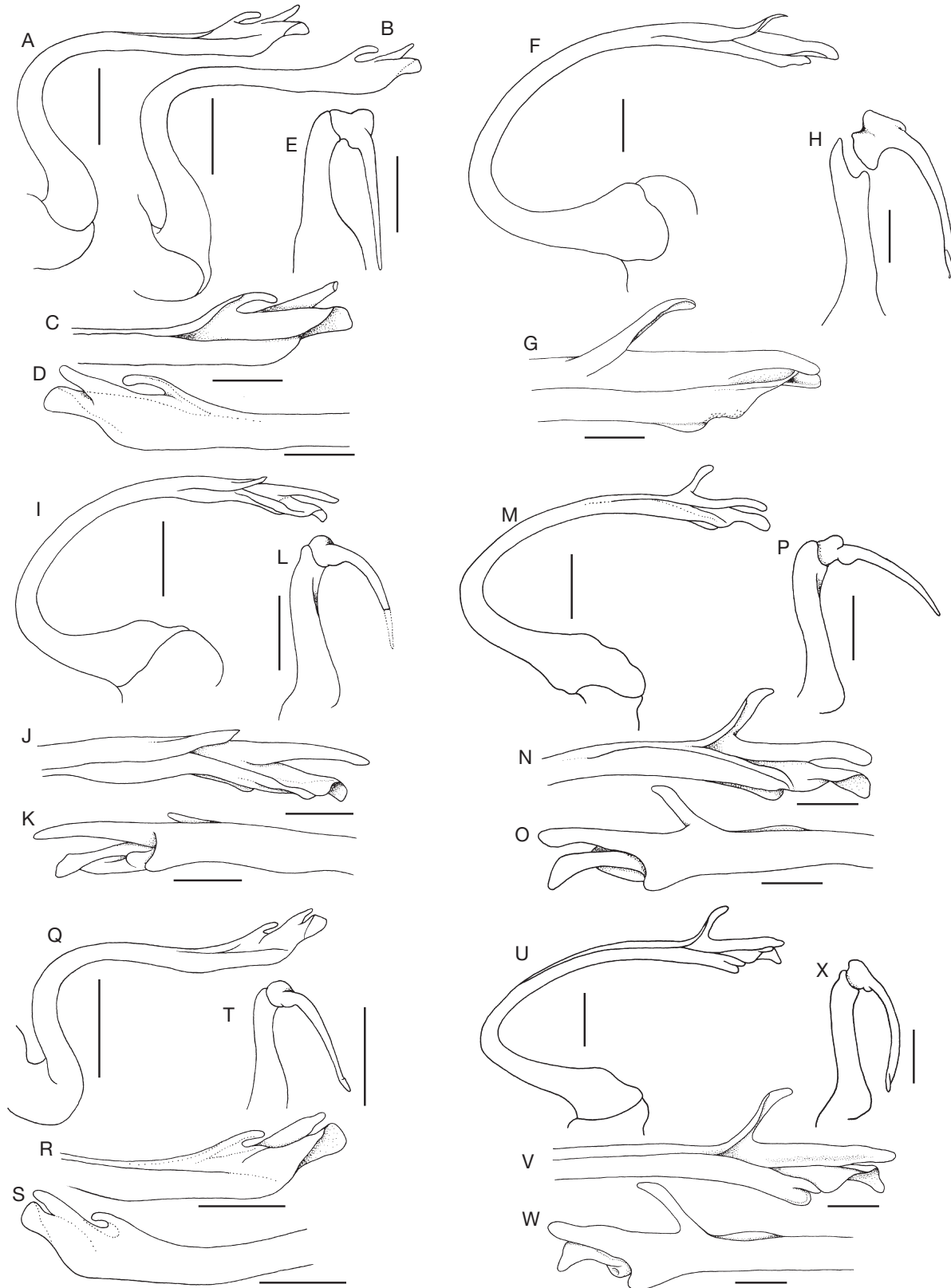


FIG. 18. — *Heikeopsis japonica* (von Siebold, 1824), typical morph, gonopods: **A–K**, ♂ 21.3×23.7 mm, Nagasaki, Japan, ZRC 1969.5.5.1; **F–H**, ♂ 22.6×24.0 mm, Kyushu, Japan, ZLKU 9425; **I–L**, ♂ 15.8×16.6 mm (holotype of *Neodorippe (Neodorippe) japonica* var. *taiwanensis* Serène & Romimontarto, 1969), Taiwan, ZRC 1969.2.24.7; **M–P**, ♂ 20.4×22.1 mm, Taiwan, ZRC 1997.0622; **Q–T**, ♂ 13.1×13.3 mm, Guangdong, southern China, ZRC 1999.0467; **U–X**, ♂ 20.3×20.9 mm, Guangdong, southern China, ZRC 1999.0469. **A, I, M, Q, U**, left G1; **B, F, H, L, P, T, X**, right G2 (ventral view); **C, J, N, R, V**, distal part of left G1 (ventral view); **D, K, O, S, W**, distal part of left G1 (dorsal view); **G**, distal part of right G1 (ventral view); **E, L, P, T, X**, left G2; **H**, right G2. Scale bars: A, B, E, F, H, I, L, M, P, Q, T, U, X, 1.0 mm; C, D, G, J, K, N, O, R, S, V, W, 0.5 mm.

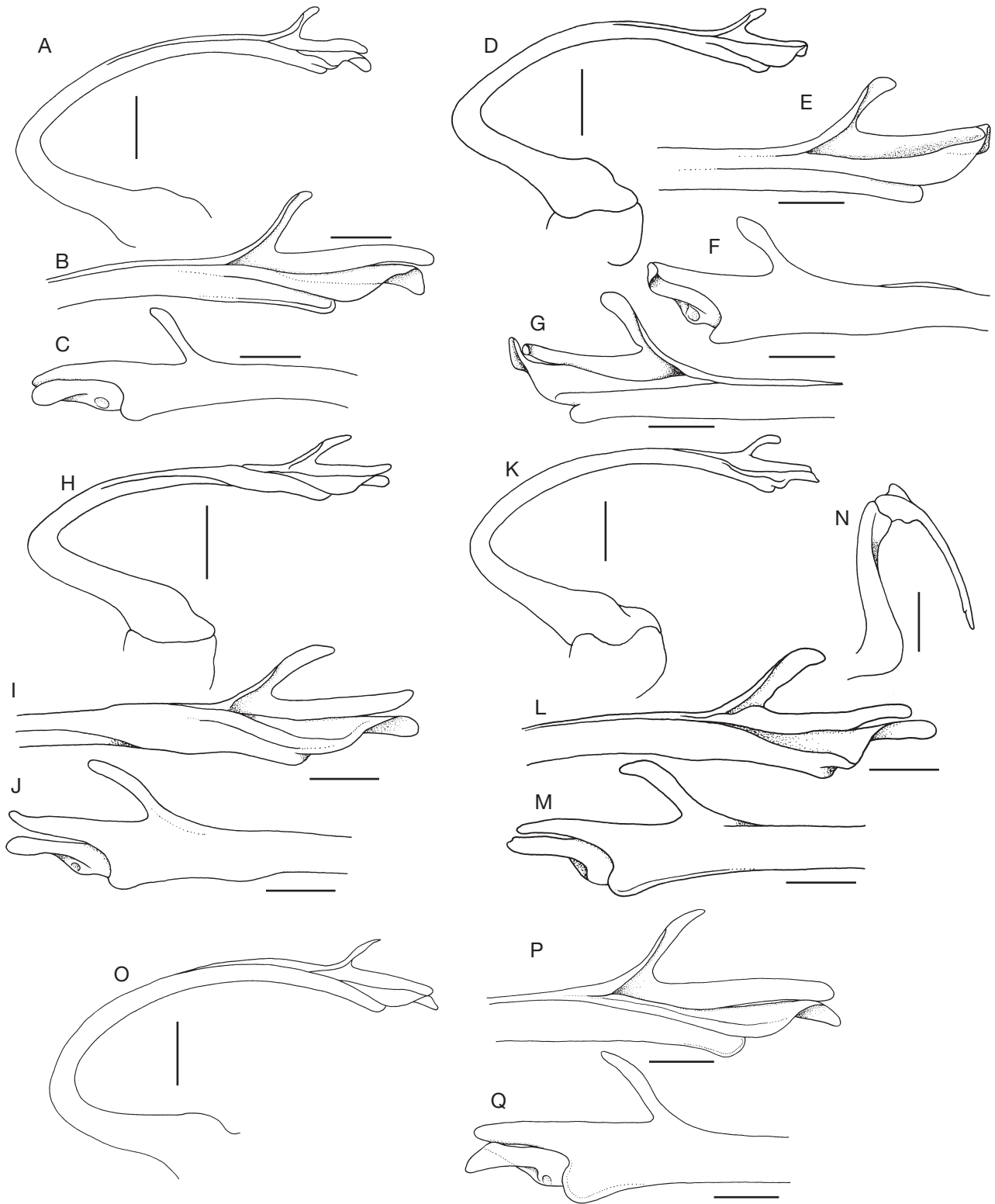


FIG. 19. — *Heikeopsis japonica* (von Siebold, 1824), gonopods: **A-G**, typical morph; **H-Q**, short-legged morph. **A-C**, ♂ 20.8×22.1 mm, Hong Kong, southern China, ZRC 2021.0744; **D-G**, ♂ 20.3×20.6 mm, Hong Kong, southern China, ZRC 2021.0748; **H-J**, ♂ 18.8×19.0 mm, Shanghai, northern China, ZRC 1998.0330; **K-N**, ♂ 21.9×24.0 mm, Qingdao, northern China, ZRC 2002.0491; **O-Q**, ♂ 15.7×16.2 mm, Korea, SNUC 271101#005. **A, D, H, K, O**, left G1 (ventral view); **B, E, I, L, P**, distal part of left G1 (ventral view); **C, E, J, M, Q**, distal part of left G1 (dorsal view); **G**, distal part of right G1 (ventral view); **N**, left G2. Scale bars: A, D, H, K, N, O, 1.0 mm; B, C, E-G, I, J, L, M, P, Q, 0.5 mm.

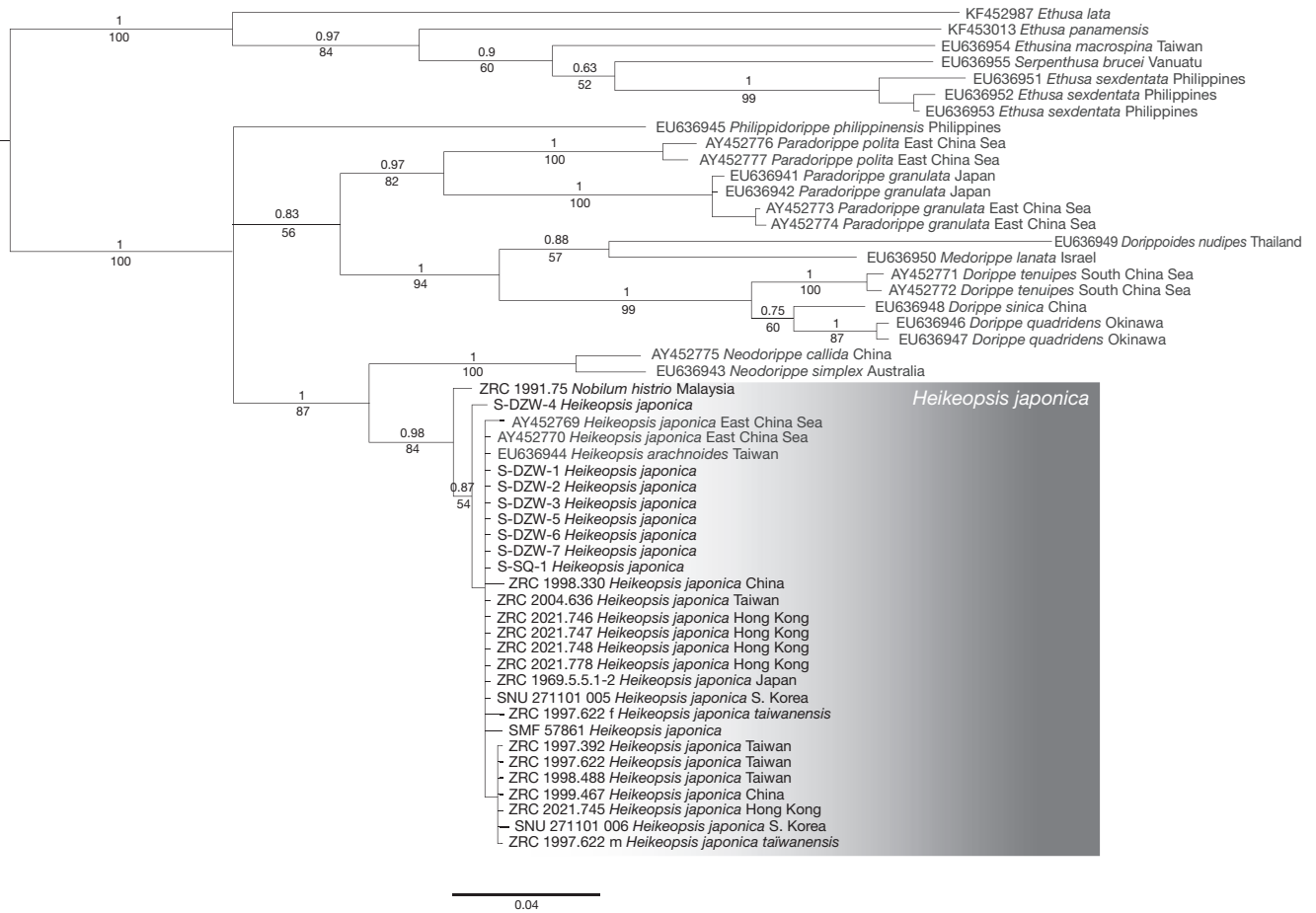


FIG. 20. — Phylogenetic tree obtained from the mitochondrial 16S rRNA marker by Bayesian Inference. Numbers above branches represent Bayesian posterior probabilities, numbers under branches are Maximum Likelihood bootstrap values. Newly produced sequences are in black, sequences retrieved from GenBank are in grey. Sequences of *Heikeopsis japonica* as defined by the species delimitation analysis (see Fig. 21) are highlighted by the grey box.

We are less certain about the population from Korea as we have only two specimens. The material of Kamita (1934: fig. 1; 1941a: fig. 6; see also Kamita 1935: 62, no figure, all as *Dorippe japonica*) and Ko & Lee (2013: 19, figs 10, 11) from Korea appear to have relatively shorter P2 and P3 and are closer to the condition of the short-legged form. Kim (1973: 610, pl. 76, fig. 57a, b; figs 85, 87, as *Neodorippe (Neodorippe) japonica*), however, figured the species from Korea, and his photograph of the overall adult habitus (pl. 76, fig. 57a, b) appears to show relatively longer P2 and P3. This is also the case for the specimens we have examined from Korea (Fig. 6G, H). All the specimens on hand (including the one figured in Kim 1973) appear to be relatively small (less than 17 mm in carapace length), with none possessing the swollen major chela of large males, and we do know that subadults have relatively longer legs in typical *H. japonica* (e.g., Fig. 14C, D). On the basis of these observations at least, we believe Korea has the short-legged morph, which is not surprising as the country is just adjacent to northern China. On this basis,

populations from the Yellow Sea (Kamita 1934, 1935, 1936), Korea Strait (Kamita 1936), Jinsen (= Incheon) (Urita 1926), Zinsen (Sakai 1937), Wido Island (Kim 1970, 1973), Busan, Jinhae, Masan, Asan, Juan, Hancheon, Nanseo, Myeon and Suun Island (Kamita 1941b), Soare [in Incheon], Biin and Gomso [in Gyeonggi] in South Korea (Kim & Kim 1982) probably also belong to the short-legged morph.

MOLECULAR APPROACH

Both 16S and COI were sequenced but 16S had a higher PCR success rate and thus gave the largest dataset to use for this analysis, which is why we only included this marker in our study. The analysis of the 16S rRNA fragment (Fig. 20) revealed that all the sequences from specimens of *Heikeopsis* cluster in a well-supported clade (PP = 0.98; B = 84) together with the sequence from *Nobilium histrio*. Furthermore, the ASAP species delimitation analysis (Fig. 21) supported the hypothesis that all of these sequences are conspecific in all but one of the 10 partition schemes tested.

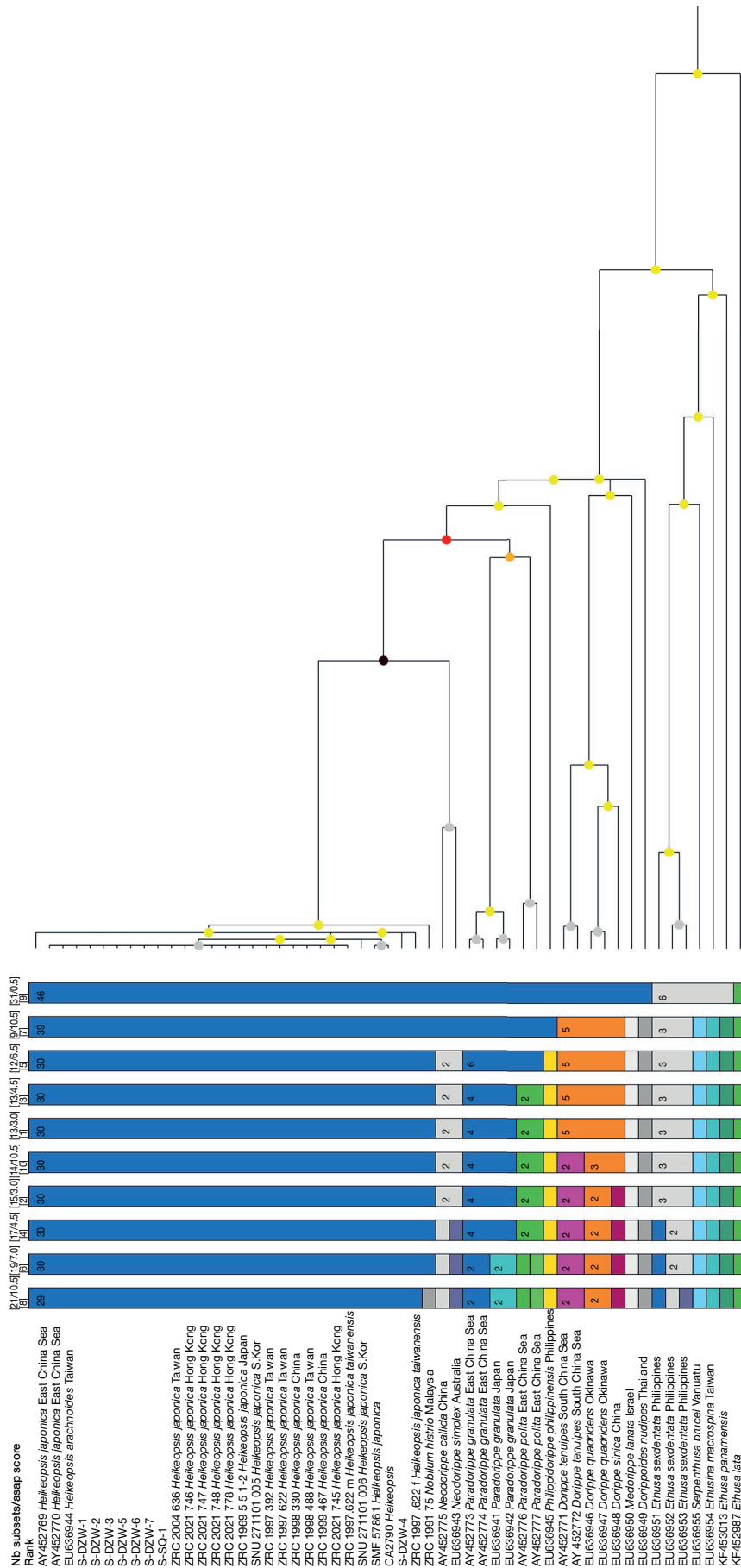


FIG. 21. — Partitions obtained from the ASAP species delimitation analysis on the 16S dataset. Different colours indicate different species according to each partition (vertical boxes) of the phylogenetic tree (right).

DISCUSSION

In the revision of Holthuis & Manning (1990), the relative length of the legs P2 and P3, in particular that of the merus, is a criterion often used for specific morphological differentiation and has proven to be a reliable character in most cases. Given that this could be a sexually dimorphic trait, as is the case for the setation of P2 and P3 in some dorippids, it may be necessary to distinguish the condition in both sexes (Guinot 2023). In most dorippids, leg length differences are associated with other morphological differentiation criteria. For example, *Dorippe tenuipes* Chen, 1980, which can be distinguished from all other species of *Dorippe* Weber, 1795 by very long and slender legs, with a P3 merus almost 7 times as long as high (compared to the short-legged species *D. quadridens* (Fabricius, 1793) and *D. sinica* Chen, 1980, with a P3 merus 4 to 4.5 times as long as high), differs from all of them, among others, by the more developed callosity at the base of P3 (Guinot 2023: figs 9D, 33G, H). The P2 and P3 may not be sexually dimorphic in size as, e.g., in *Dorippoides* Serène & Romimohtarto, 1969 and *Paradorippe* Serène & Romimohtarto, 1969, whereas sexual dimorphism in leg length, especially of the merus, occurs in *Philippidorippe* Chen, 1986, where P2 and P3 are significantly proportionally shorter and stouter in females than in males (Guinot 2023: fig. 27A, B). In her review of the Dorippidae, Guinot (2023), who examined a rather large number of individuals in several species, taking into account that populations can show considerable variation in body size at sexual maturity, did not find significant variability among conspecific individuals.

This is not the case for the crab known under the specific name *japonica*, assigned to *Dorippe*, *Neodorippe*, *Nobilium*, *Heikea* or *Heikeopsis*, which Holthuis & Manning (1990: 72, key 80) described as having the 'Merus of P3 less than 6.3 times longer than high' and with 'Second and third legs slender, long, both reaching beyond front with distal end of merus'. In fact, their *Heikea japonica* includes specimens from Japan, China, Korea, Taiwan and Vietnam with P2 and P3 of eminently variable length, ranging from short and stout to long and thinner, a feature that, according to these authors, seems to fall within the range of variation of this species. We saw above the confusion that ensued.

The observation that there are apparently two forms of *H. japonica*, one usually with relatively longer P2 and P3 as adults (the typical morph), and another with relatively shorter legs is noteworthy. More so since the typical morph of *H. japonica* has a wide distributional range, from northern Japan to Taiwan, Hong Kong and Vietnam; while the shorter-legged morph is known only from northern China (Shanghai to Qingdao) and Korea. There is also no obvious sexual dimorphism in leg proportions for *H. japonica*.

We do not know to what extent long-legged and short-legged populations are sympatric. *Heikeopsis japonica* as defined here (including the synonyms and the short-legged morph) is a sublittoral species, rarely found in deeper waters, occurring at depths of 15–92 m (Manning & Holthuis 1986), up

to 132 m (Yokoya 1933; Sakai 1937; Horikoshi *et al.* 1982). As far as is known, typical *H. japonica* and the short-legged morph occur in similar habitats. There is also no obvious sexual dimorphism in leg proportions for *H. japonica*.

An observation on how dorippids bury (and not burrow, see Bellwood 2002) is useful here. Dorippids practice rapid forward burying, i.e., they actively move through the substrate and dig into sediment with their bodies and first two ambulatory legs, combining both carrying and burying behaviours. With regard to the longer or shorter (or more slender or stouter) meri of the ambulatory legs examined in this study, we do not know if their relative lengths assist in the burying behaviour. Field videos clearly show dorippids (with an organism carried by P4 and P5 covering most of the carapace) walking forward, also using their chelipeds to walk, then burying forward. As opposed to sideways locomotion considered to be the attribute of brachyuran crabs, the forward locomotion of dorippids with the chelipeds (sometimes mixed with phases of lateral locomotion) – thus using chelipeds as a special pair of 'walking legs' is a plesiomorphic behaviour, comparable to that of dromiids. *Medorippe lanata* (Linnaeus, 1767) moves quite quickly and leaps while pushing with its long P3, while the P2 are useful for balancing the weight of the carried object in relation to its body (Bedini *et al.* 2003).

Intra-specific polymorphism has been reported in other decapods, namely freshwater atyid shrimps of the genera *Caridina* H. Milne Edwards, 1837 (de Mazancourt *et al.* 2017) and *Macrobrachium* Spence Bate, 1868 (Zimmermann *et al.* 2012) in which important taxonomic characters like the length of the rostrum or of some articles of the pereopods were correlated with the habitat, following an altitudinal gradient (de Mazancourt *et al.* 2017). It is known that some subtle ontogenetic changes can be affected by diet and environmental conditions (e.g., for the grapsid *Goniopsis cruentata* (Latreille, 1803), see Soares-Silva *et al.* 2024: fig. 8 [graph]). A similar situation is not yet known for brachyuran crabs and, to our knowledge, a case of leg length variation in adult brachyuran crabs has not been reported in the literature. The case of the inachoidid genus *Leurocyclus* Rathbun, 1897, from Brazil, Argentina and Chile, is interesting to note. The two previously recognised species, *L. tuberculosus* (H. Milne Edwards & Lucas, 1842) with stout merus on P2–P4, especially P2, and *L. gracilipes* (A. Milne Edwards & Bouvier, 1923) with slender and long merus on these same legs, in fact correspond to an allometric variation in a same and unique species: the first (*tuberculosus*) represents the adult male, and the second (*gracilipes*) represents the juvenile, female and young adult stages. As such, there is only one species, *L. tuberculosus*, the type species of the monotypic genus *Leurocyclus* (see Guinot 1984). On the other hand, the simultaneous presence of long/thin and short/stout legs observed in adults of the same species may imply the presence of a puberty terminal moult (as in majoids) that, within the range of a species or even a population, may be achieved by individuals after a variable number of moult instars and thus with a difference in size at morphometric maturity (Hartnoll 1974).

The fact that populations of *Heikeopsis japonica* show slight and intergrading morphological differences, with only one character, the P2 and P3 length and shape, allowing distinction, is perhaps the result of incipient fragmentation or early cladogenesis. A widely distributed *H. japonica*, with more or less continuous gene exchange and clinal intergradation, could have split into two or more populations, and the resulting populations or sets of populations may not have diverged and are the remains of an ancestrally continuous population (the differences being the result of the disappearance of intermediate populations). França *et al.* (2024) discussed this with regards to the western Atlantic panopeid *Eurytium limosum* (Say, 1818) when they observed subtle morphological differences in the chelipeds and gonopods but could not discern a biogeographic pattern, and this morphological variability was genetically unsupported. They concluded that “Neither molecular nor morphological data indicated marked variations that would support the interruption of gene flow or phylogeographic division among representative specimens of the evaluated provinces. The existing and observed variations did not present a pattern associated with greater genetic distance or geographic proximity to the provinces or locations from which the samples were collected. In conclusion, it is suggested that the variation in biotic and abiotic conditions between the different provinces sampled does not represent barriers to gene flow between individuals of *E. limosum* populations.” (França *et al.* 2024: 12). In the case of the short- versus long-legged morphs of *H. japonica*, as noted above, we do not know of any habitat differences that can explain the differences.

There have been various reports of a north-south divide for species groups for various intertidal brachyurans of the families Ocypodidae Rafinesque, 1815, Varunidae H. Milne-Edwards, 1853 and Sesarmidae Dana, 1851, although the patterns of distribution are not always the same. The distribution patterns of the varunids, *Eriocheir sinensis* H. Milne Edwards, 1853, and *E. hepuensis* Dai, 1991 (Naser *et al.* 2012, based on COI), the sesarmids, *Orisarma dehaani* (H. Milne Edwards, 1853) and *O. neglectum* (De Man, 1887) (Schubart & Ng 2020, based on 16S, tRNA-Leu and ND1), and the ocypodids *Paraleptuca crassipes* (White, 1847) and *P. splendida* (Stimpson, 1858) (Shih *et al.* 2012, based on COI), are similar to that of the long- and short-legged *H. japonica*, with the species north and south of the Taiwan Strait closely resembling each other but currently regarded as separate species. In these cases, however, there are subtle and consistent morphological differences between the populations on two sides of the strait to support recognising them as different. There is genetic evidence for recognising two populations for *Eriocheir* De Haan, 1835 and *Paraleptuca* Bott, 1973 (Naser *et al.* 2012; Shih *et al.* 2012) but for *Orisarma* Schubart & Ng, 2020, there is none, with Schubart & Ng (2020: 912) commenting that “In the current genetic dataset, there are no obvious genetic differences between *O. magnum* [(Komai & Ng, 2013)], *O. neglectum* and *O. dehaani*, which should normally be expected for intraspecific relationships. We see a similar pattern for the closely related *O. intermedium* [(De

Haan, 1835)] and *O. sinense* [(H. Milne Edwards, 1853)]. The morphological differences, however, are such that all three of them must be recognised as distinct species.”

In summary, it is possible that the northern Chinese population of *H. japonica*, with its typically short adult P2 and P3, is in the early stages of being isolated, like the above varunid, ocypodid and sesarmid species, but not long enough for obvious morphological differences to develop or for substantial genetic differences to be accumulated, at least for the gene markers now used. What is here perceived as incipient evolution may of course be also due to our current failure to find useful morphological discriminators to recognise them, and/or to select the right genetic markers that may have captured the phylogenetic event. That is something that must be examined again in the future.

Acknowledgements

We have to thank many colleagues for their kind help. Paul Clark (NHM) helped us search for the material of *Heikeopsis arachnoides* and Kevin Webb (Photography Unit) kindly helped take the necessary photographs of the specimens. Charles Fransen kindly helped us photograph material, and later facilitated the study of the specimens by us, including lectotype and paralectotypes of *H. japonica*; and in Japan, So Ishida, Fumio Takeshita and Hidenori Yosigou gave us access to OMNH, ZLKU and HMNH specimens, respectively. We thank Li Xinsheng, from the Chinese Academy of Sciences in Qingdao, for generously helping us collect specimens, take photographs of fresh specimens, sequencing the material, generously sharing this data with us and donating specimens to MNHN and ZRC. We are also most grateful to Kingsley Wong (Hong Kong) as well as Ko Hyun Suk and Lee Sang-Kyu (Korea) who sent us specimens from Hong Kong and Korea, respectively. We would like to thank Angelika Brandt (Senckenberg Research Institute and Natural History Museum), assisted by the curatorial team in this institution (Bianca Trautwein and Kristin Arnold), who offered the first author the loan of the material of unidentified Dorippidae from the SMF, which is very rich in *Heikeopsis japonica* native to Japan, one specimen of which was sequenced. Lee Bee Yan (ZRC) and Sébastien Soubzmaigne (MNHN) helped take photographs of some of the specimens in the ZRC and MNHN, respectively. For some colour photographs of material from Taiwan, we thank Chan Tin-Yam and Huang Jung-Fu. Martyn Low helped for PDFs, Paula Martin-Lefèvre (MNHN, Direction des Collections) for valuable curatorial support, and Laure Corbari (Curator of the Crustacean collection, MNHN) for access to the collections. We express our deepest gratitude to the two reviewers, Charles H. J. M. Fransen and Jose Christopher E. Mendoza, who examined our manuscript very carefully and whose corrections and suggestions allowed us to greatly improve it. The last author was supported by a postdoctoral fellowship of the Alexander von Humboldt Foundation at the Museum für Naturkunde-Leibniz Institute for Evolution and Biodiversity Science in Berlin (Germany), where part of the molecular analyses were performed.

REFERENCES

- ANONYMOUS 1904. — Zoological Part, in *National Monuments of Ishikawa Prefecture*: i-vii, 1-92, pls 1-88. [Crabs, including Lithodidae: 47-92, pls 45-79.]
- BALSS H. 1922. — Die Dromiaceen, Oxystomen und Parthenopiden. Ostasiatische Decapoden, III. *Archiv für Naturgeschichte* 88, Abteilung A, Heft 3: 104-140.
- BEDINI R., CANALI M. G. & BEDINI A. 2003. — Use of camouflaging materials in some brachyuran crabs of the Mediterranean infralittoral zone. *Cahiers de Biologie Marine* 44: 375-383.
- BELLWOOD O. 2002. — The occurrence, mechanics and significance of burying behaviour in crabs (Crustacea: Brachyura). *Journal of Natural History* 36 (10): 1223-1238. <https://doi.org/10.1080/00222930110048891>
- CHANG C.-M. 1963. — A check-list of Taiwan crabs with descriptions of 19 new records. *Biological Bulletin of the Tunghai University* 14: 1-23.
- CHEN H. 1980. — Two new species of crabs from South China Sea. *Oceanologia et Limnologia Sinica* 11 (2): 154-160, pls 1-2. (In Chinese with English abstract).
- CHEN H. 1986. — Studies on the Dorippidae (Crustacea, Brachyura) of Chinese waters. *Transactions of the Chinese Crustacean Society* 1: 118-139. (In Chinese with English abstract).
- CHEN H. & SUN H. 2002. — Brachyura. Marine primitive crabs, in *Fauna Sinica, Invertebrata*, vol. 30. *Arthropoda, Crustacea*. Academia Sinica, Science Press, Beijing, China, xiii + 597 p. (In Chinese with English abstract). <https://www.biodiversitylibrary.org/part/119053>
- DAI A. & YANG S. 1991. — *Crabs of the China Seas*. China Ocean Press, Beijing and Springer-Verlag, Berlin Heidelberg New York Tokyo, English edition. (Translation from Chinese original 1986): 1-682, figs 1-295, pls 1-74.
- DAI A.-Y., YANG S.-L., SONG Y.-Z. & CHEN G.-X. 1986. — *Crabs of the China Seas*. China Ocean Press, Beijing, 11 + 642 p. (In Chinese).
- DARRIBA D., TABOADA G. L., DOALLO R. & POSADA D. 2012. — JModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9 (8): 772. <https://doi.org/10.1038/nmeth.2109>
- DAVIE P. J. F., GUINOT D. & NG P. K. L. 2015. — Anatomy and functional morphology of Brachyura (Chapter 71-2), in CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology. Vol. 9C-I*. Brill, Leiden and Boston: 11-163. https://doi.org/10.1163/9789004190832_004
- DAWYDOFF M. C. 1952. — Contribution à l'étude des invertébrés de la faune marine benthique de l'Indochine. *Bulletin biologique de la France et de la Belgique* Supplement 37: 1-158.
- DE HAAN W. 1833-1850. — Crustacea, in PH. FR. DE SIEBOLD, *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823-1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit*. Lugduni Batavorum, Leiden, 1839, fasc. 4: 73-108, pls 25-32, G, H; 1841, fasc. 5: 109-164, pls 33-37, 39-42, 47; 1849, fasc. 7: 197-243, i-xxxi. <https://biodiversitylibrary.org/page/53607674>
- DOFLEIN F. 1904. — Brachyura, in CHUN C., *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia", 1898-1899*. Vol. 6. Jena, xiv + 314 p., figs 1-68. Atlas, 58 pls. <https://www.biodiversitylibrary.org/part/119053>
- EDGAR R. C. 2004. — MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32 (5): 1792-1797. <https://doi.org/10.1093/nar/gkh340>
- FAN Y., LI X., SONG L. & CAI Z. 2004. — Phylogenetic relationships of five species of Dorippinae (Crustacea, Decapoda) revealed by 16S rDNA sequence analysis. *Acta Oceanologica Sinica* 23 (3): 513-519.
- FAUVEL A.-A. 1880. — Promenades d'un naturaliste dans l'archipel des Chusan et sur les côtes du Chekiang (Chine). (Suite). *Mémoires de la Société des Sciences naturelles et mathématiques* (Cherbourg) 23: 29-201, 2 pls.
- FELSENSTEIN J. 1985. — Confidence Limits on Phylogenies: An Approach Using the Bootstrap. *Evolution* 39 (4): 783. <https://doi.org/10.2307/2408678>
- FOLMER O., BLACK M., HOEH W., LUTZ R. & VRIJENHOEK R. 1994. — DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3 (5): 294-299. https://www.mbari.org/wp-content/uploads/2016/01/Folmer_94MMBB.pdf
- FRANÇA N. F. C., SANTOS E. F. & MANTELATTO F. L. 2024. — Genetic and morphological variability of *Eurytium limosum* (Say, 1818) (Brachyura, Panopeidae): insights about dispersal along marine provinces. *Thalassas* 2024: 1-14. <https://doi.org/10.1007/s41208-023-00658-y>
- FRANSEN C. H. J. M., HOLTHUIS L. B. & ADEMA J. P. H. M. 1997. — Type-Catalogue of the Decapod Crustacea in the collections of the Nationaal Natuurhistorisch Museum, with appendices of pre-1900 collectors and material. *Zoologische Verhandlungen* 311: i-xvi, 1-344.
- GUINOT D. 1984. — Le genre *Leurocyclus* Rathbun, 1897 (Crustacea Decapoda Brachyura). *Bulletin du Muséum national d'Histoire naturelle 4^e sér.* 6 sect. A (2): 377-395. <https://www.biodiversitylibrary.org/page/58417284>
- GUINOT D. 2023. — A new subfamily classification of the highly diversified Dorippidae H. Milne Edwards, 1837 (Crustacea, Brachyura, Dorippoidea), using morphological, molecular and palaeontological data, with special emphasis on its unique female reproductive system. *Zoosystema* 45 (9): 225-372. <https://doi.org/10.5252/zoosystema2023v45a9>. <http://zoosystema.com/45/9>
- HARTNOLL R. G. 1974. — Variation in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). *Crustaceana* 27 (2): 131-136. <https://www.jstor.org/stable/20102127>
- HERKLOTS J. A. 1861. — Symbolae Carcinologicae. I. Catalogue de Crustacés qui ont servi de base au système carcinologique de M. W. de Haan, rédigé d'après la collection du Musée des Pays-Bas et les Crustacés de la faune du Japon. *Tijdschrift voor Entomologie* 4: 116-156. [Also issued separately under the title: *Symbolae Carcinologicae. Étude sur la classe des Crustacés*: 1-43].
- HOLTHUIS L. B. 1953. — On the dates of publication of W. De Haan's volume on the Crustacea of P. F. von Siebold's "Fauna Japonica". *Journal of the Society for the Bibliography of Natural History* 3 (1): 36-46.
- HOLTHUIS L. B. & MANNING R. B. 1990. — Crabs of the subfamily Dorippinae MacLeay, 1838, from the Indo-West Pacific Region (Crustacea: Decapoda: Dorippidae). *Researches on Crustacea Special no. 3*: i-iii, 1-151.
- HOLTHUIS L. B. & SAKAI T. 1970. — *Ph. F. von Siebold and Fauna Japonica; A History of Early Japanese Zoology*. Academic Press of Japan, Tokyo, i-xviii + 323 p., 38 pls, 1 map, frontispiece. (In English and Japanese). <https://www.biodiversitylibrary.org/bibliography/162655>
- HORIKOSHI M., FUJITA T., TAKEDA M., OKIYAMA M., OHTA S., TSUCHIDA E. & YAMAMOTO M. 1982. — Preliminary Compilation of the Results Obtained by the "Survey of Continental Shelf Bordering Japan" Carried out on Board the S/S Sôyô-Maru during 1923-1930, in HORIKOSHI M. (ed.), *Report for a part of Grant-in-Aid for Co-operative Research (A), Ministry of Education, Science and Culture: "Studies on Off-Shore and Deep-Sea Faunas in the West Pacific and Indian Oceans"*. Ocean Research Institute, University of Tokyo: i-xxiii, 1-252, photos & maps n.n.
- HUELSENBECK J. P. & RONQUIST F. 2001. — MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17 (8): 754-755. <https://doi.org/10.1093/bioinformatics/17.8.754>
- IHLE J. E. W. 1916. — Die Decapoda Brachyura der Siboga-Expedition. II. Oxystomata, Dorippidae. *Siboga Expeditie* 39b1, livr. 78: 97-158. <https://www.biodiversitylibrary.org/bibliography/13009>

- IMAJIMA M., UMEBAYASHI A. & OKUTANI H. 1970. — *Life in the water*. Tokyo: 1-192.
- ISBERG O. 1934. — *Studien über Lamellibranchiaten des Leptaenakalkes in Dalarna. Beitrag zu einer Orientierung über die Muschel fauna im Ordovicium und Silur*. Hakan Ohlssons, Lund: 492 p., 32 pls. <https://paleoarchive.com/literature/Isberg1934-StudienLamellibranchiatenLeptaenakalkesDalarna.pdf>
- ISHIKAWA PREFECTURE 1928. — Zoological Part, in *National Monuments of Ishikawa Prefecture*: i-vii, 1-92, pls 1-88. [Crabs, including Lithodidae: 47-84, pls 46-79.]
- ITANI G. & FUJIHARA H. 2001. — Carrying behaviour in a dorippid crab *Heikea japonica* (Arthropoda, Decapoda) – utilization of the sea pen (Cnidaria, Pennatulacea). *Nankiseibutu* 43: 47-49. (In Japanese with English Abstract).
- IVES J. E. 1891. — Echinoderms and Arthropods from Japan. *Proceedings of the Academy of Natural Sciences of Philadelphia*: 210-223. <https://www.biodiversitylibrary.org/part/84955>
- KAMITA T. 1934. — On the Genus *Dorippe* of Korea. *Zoological Magazine (Dobutsugaku Zasshi)* 46: 540-543. (In Japanese).
- KAMITA T. 1935. — On the Brachyura of the West Korean waters (Yellow Sea). *Zoological Magazine (Dobutsugaku Zasshi)* Tokyo, 47: 61-69. (In Japanese and English summary).
- KAMITA T. 1936. — Crabs from the coast of Korea Strait. *Journal of the Chosen natural History Society* 21: 30-35. (In Japanese).
- KAMITA T. 1941a. — *Studies of the Decapod Crustaceans of Chosen. Pt. I. Crabs*. The Fisheries Society of Chosen, Keijo: 1-289, figs 1-147, 2 pls, 1 map.
- KAMITA T. 1941b. — On the distribution of brachyuran Crustacea in Korea. *Zoological Magazine (Dobutsugaku Zasshi)* 53 (5): 232-244.
- KAMITA T. 1963. — Crabs of San-in District, including Oki Islands and its adjacent waters (Southern part of Japan Sea). *Researches on Crustacea* 1: 20-31, figs 1-7.
- KANEKO S. 1958. — *Crustacean Remains from the Holocene Deposits in Osaka City* (Pt. 1), in Jubilee Publication in the Commemoration of Professor H. Fujimoto Sixtieth Birthday: 331-339, pl. 15. (In Japanese).
- KHIM J. S., LEE C., SONG S. J., BAE H., NOH J., LEE J., KIM H.-G. & CHOI J. W. 2021. — Marine Biodiversity in Korea: a review of macrozoobenthic assemblages, their distributions, and long-term community changes from human impacts. *Oceanography and Marine Biology: An Annual Review* 59: 483-532. CRC Press. <https://doi.org/10.1201/9781003138846-6>
- KIM H. S. 1970. — A checklist of the Anomura and Brachyura (Crustacea, Decapoda) of Korea. *Seoul University Journal, Biology and Agriculture (Series B)* 21: 1-34, fig. 1, pls 1-5.
- KIM H. S. 1973. — A Catalogue of Anomura and Brachyura from Korea, in *Illustrated Encyclopedia of Fauna and Flora of Korea*, Samhwa Publishing Company, 14: 1-694, figs 1-265, pls 1-112, tabs 1-2, 1 map. Seoul. (In Korean with English summary).
- KIM H. S. 1977. — A fauna-list of the Decapod Crustaceans of Korea, in *Commemoration Papers for Professor M.J. Lee*: 199-208.
- KIM W. & KIM H. S. 1982. — Classification and geographical distribution of Korean crabs (Crustacea, Decapoda, Brachyura). *Proceedings of the College of Natural Sciences*, Seoul National University 7: 133-159.
- KIM H. S., LEE K. S., KIM W. & KWON D. H. 1981. — A faunal and ecological study on the crustaceans in the intertidal zones near Incheon and southern part of Ganghwa Island. *Bulletin of the Korean Association for Conservation of Nature, Series III*: 279-309. (In Korean, with English summary).
- KO H.-S. & LEE S.-H. 2013. — Invertebrate Fauna of Korea, vol. 21, no 30, in *Fauna and Flora of Korea. Crabs and Zoaea. III Arthropoda: Malacostraca: Decapoda: Brachyura: Cancridae, Cheiragonidae, Dorippidae, Euryplicidae, Goneplacidae, Hymenosomatidae, Portunidae*. National Institute of Biological Resources, Ministry of Environment, 77 p.
- KOZLOV A. M., DARRIBA D., FLOURI T., MOREL B. & STAMATAKIS A. 2019. — RAXML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics* 35 (21): 4453-4455. <https://doi.org/10.1093/BIOINFORMATICS/BTZ305>
- LEE S.-K., LEE C., NOH J., SONG S. J. & KHIM J. S. 2021. — First comprehensive ecological checklist of Brachyura in Korea: 1879-2020. *Marine Pollution Bulletin* 171: 112742.
- LIN C. C. 1949. — A catalogue of Brachyurous Crustacea of Taiwan. *Quarterly Journal of the Taiwan Museum* 2 (1): 10-33.
- LUQUE J., XING L., BRIGGS D. E. G., CLARK E. G., DUQUE A., HUI J., MAI H. & MCKELLAR R. C. 2021. — Crab in amber reveals an early colonization of nonmarine environments during the Cretaceous. *Science Advances* 7: eabj5689. <https://doi.org/10.1126/sciadv.abj5689>
- LUO X., REN Y., XING L. & XU B. 2015. — Species composition and diversity of crab assemblage in Haizhou Bay. *Biodiversity Science* 23 (2): 210-216. <https://doi.org/10.17520/biods.2014205>
- MACHIDA Y., ENDO H., YAMAMOTO A. & WATANABE H. 2009. — Brachyurans collected by gill nets from Urado Bay, in *Comprehensive study of Kochi City. 1. Nature of the regions*: 535-562 (including 10 pls). Kochi City, Kochi, 604 p. https://www.city.kochi.kochi.jp/uploaded/life/133358_434756_misc.pdf
- MAKI M. & TSUCHIYA H. 1923. — *Illustrated reports of the crustacean decapods from Formosa*. Report of the Department of Agriculture, Government of Research Institute of Taihoku, No. 3: 1-215. (In Japanese).
- MANNING R. B. & HOLTHUIS L. B. 1981. — West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* 306: i-xii, 13-379. <https://doi.org/10.5479/si.00810282.306>
- MANNING R. B. & HOLTHUIS L. B. 1986. — Preliminary descriptions of four new species of dorippid crabs from the Indo-west Pacific region (Crustacea: Decapoda: Brachyura). *Proceedings of the Biological Society of Washington* 99 (2): 363-365. <https://biostor.org/reference/75013>
- MARTIN J. W. 1993. — The Samurai Crab. *Terra* 31 (4): 30-34. <https://isopods.nhm.org/pdfs/3729/3729.pdf>
- MARUMURA M. & KOSAKA A. 2003. — Catalogue of the Brachyuran and Anomuran Crabs donated by the Late Mr. Seiji Nagai to the Wakayama Prefecture Museum of Natural History. *Wakayama Natural History Museum, Wakayama*: 73 p. (In Japanese).
- MAZANCOURT V. DE, MARQUET G. & KEITH P. 2017. — The “Pinocchio-shrimp effect”: First evidence of variation in rostrum length with the environment in *Caridina* H. Milne-Edwards, 1837 (Decapoda: Caridea: Atyidae). *Journal of Crustacean Biology* 37 (3): 249-257. <https://doi.org/10.1093/jcbl/rux025>
- MIERS E. J. 1886. — Report on the Brachyura collected by H.M.S. *Challenger* during the years 1873-1876, in THOMPSON C. W. & MURRAY J. (eds), *Report on the Scientific Results of the exploring Voyage of H.M.S. Challenger during the years 1873-1876, under the command of Captain George S. Nares, R.N., F.R.S. and the Late Captain Frank Tourle Thomson, R.N.* Zoology 17 (2): i-xli, 1-362, pls 1-29. <https://doi.org/10.5962/bhl.title.6513>
- MILLER M. A., PFEIFFER W. & SCHWARTZ T. 2010. — Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*: 1-8. <https://doi.org/https://doi.org/10.1109/GCE.2010.5676129>
- MIYAKE S. 1961a. — Fauna and Flora of the Sea around the Amakusa Marine Biological Laboratory. Part II. Decapod Crustacea. *Amakusa Marine Biological Laboratory, Kyushu Univ. Publ.*: i-iv, 1-30. (In Japanese).
- MIYAKE S. 1961b. — A list of the decapod Crustacea of the Sea of Ariake, Kyushu. *Records of Oceanographic Works in Japan Spec. No. 5*: 165-178.
- MIYAKE S. 1983. — Brachyura (Crabs). *Japanese Crustacean Decapods and Stomatopods in Color*. Volume 2: i-viii, 1-277, plates 1-64. Hoikusha, Osaka. (In Japanese; second edition in 1992)
- MIYAKE S. & TAKEDA M. 1978. — Suborder Brachyura, in KIKUCHI T. & MIYAKE S. (eds), *Fauna and Flora of the Sea*

- Around the Amakusa Marine Biological Laboratory, Part II. Decapod Crustacea (Revised [sic] Edition). Contributions of the Amakusa Marine Biological Laboratory of Kyushu University, 245: 32-45. (In Japanese and English).
- MIYAKE S., SAKAI K. & NISHIKAWA S. 1962. — A fauna-list of the decapod Crustacea from the coasts washed by the Tsushima Warm Current. *Records of Oceanographic Works in Japan* Special no. 6: 121-131. <https://research.nhm.org/pdfs/19956/19956.pdf>
- MORITA S. 1977. Decapoda, in BABA Y. (ed.), *The Fossils Excavated in Aichi Prefecture, Japan (The First Series). The Alluvial Fauna Discovered in the Artificial Land of Reclaimed Sand Around the Nagoya Port*. Tokai Fossil Society, Nagoya: 10-63.
- MURAOKA K. 1998. — Catalogue of the Brachyuran and Anomuran Crabs donated by Prof. Dr. Tane Sakai to the Kanagawa Prefectural Museum. *Catalogue of the Collection in the Kanagawa Prefectural Museum of Natural History* 11: 5-67, pls 1-16.
- MURAOKA K. & KONISHI K. 1988. — Bibliography on the larvae of decapod Crustacea of Japan - Brachyura (1). *Aquabiology* 10 (2): 124-127. (In Japanese with English summary).
- NASER M. D., PAGE T. J., NG N. K., APEL M., YASSER A. G., BISHOP J. M., NG P. K. L. & CLARK P. F. 2012. — Invasive records of *Eriocheir hepuensis* Dai, 1991 (Crustacea: Brachyura: Grapsoidea: Varunidae): implications and taxonomic considerations. *BioInvasions Records* 1 (1): 71-86. <https://doi.org/10.3391/bir.2012.1.1.15>
- NEES VON ESENBECK C. G. D. 1825. — De Historiae naturalis in Japonia statu, nec non de augmento emolumentisque in decursu perscrutationum exspectandis, Dissertatio cui accedunt Spicilegia Faunae Japonicae. Batavia. 1824. *Bulletin universel des sciences et de l'industrie*, Section II, Sciences naturelles et [la] géologie, Paris, 4: 86-88.
- NG P. K. L. & HUANG J.-F. 1997. — Unrecorded Crabs (Crustacea: Decapoda: Brachyura) from Taiwan and Tungsha Islands, with description of a new genus and species of Xanthidae. *Zoological Studies* 36 (4): 261-276. <https://scholarbank.nus.edu.sg/handle/10635/102115>
- NG P. K. L., WANG C.-H., HO P.-H. & SHIH H.-T. 2001. — An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Special Publication Series*, No. 11, 86 p.
- NG P. K. L., GUINOT D. & DAVIE P. J. F. 2008. — Systema Brachyurorum: Part 1. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology Supplement* 17: 1-286. [updates at <http://rmb.r.nus.edu.sg/research/cotw/supplement17.php>]
- NG P. K. L., SHIH H.-T., HO P.-H. & WANG C.-H. 2017. — An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Academic Journal* 70 (3 & 4): 1-185.
- NISHIMURA S. & SUZUKI K. 1971. — *Common Seashore Animals of Japan in color*, i-xii, 1-196, unnumbered figs, pls 1-64, maps 1-2. Hoikusha, Osaka. (In Japanese).
- PALUMBI S. R. 1996. — Nucleic acids II: The polymerase chain reaction, in PALUMBI S. R., HILLIS D. M., MORITZ C. & MABLE B. K. (eds). *Molecular systematics* 2: 205-247.
- PARISI B. 1914. — Oxystomata. I Decapodi giapponesi del Museo di Milano. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale*, Milano 53: 280-312 [p. 5-35 on separate]. <https://www.biodiversitylibrary.org/bibliography/12872>
- PUIILLANDRE N., BROUILLET S. & ACHAZ G. 2021. — ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources* 21 (2): 609-620. <https://doi.org/10.1111/1755-0998.13281>
- QUINTANA R. 1987. — Late zoeal and early postlarval stages of three dorippid species from Japan (Brachyura: Dorippidae: Dorippinae). *Publications of the Seto Marine Biological Laboratory* 32 (4-6): 233-274. https://repository.kulib.kyoto-u.ac.jp/dspace/bitstream/2433/176143/1/fia0324-6_233.pdf
- RATHBUN M. J. 1902. — Japanese stalked eyed Crustaceans. *Proceedings of the United States National Museum* 36 (1307): 23-55. <https://doi.org/10.5479/si.00963801.26-1307.23>
- RATHBUN M. J. 1931. — New and rare Chinese crabs. *Lingnan Science Journal* 8 [for 1929]: 73-104. (With p. 99 addition to Gee's List 1925).
- RONQUIST F. & HUELSENBECK J. P. 2003. — MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19 (12): 1572-1574. <https://doi.org/10.1093/bioinformatics/btg180>
- SAKAI K. & NAKANO T. 1983. — List of decapod Crustacea in Laboratory of Crustacea, Shikoku Women's University, Tokushima. I. *Bulletin of Shikoku Women's University* 3 (1): 73-94.
- SAKAI T. 1934. — *Brachyura from the Coast of Kyusyu, Japan. Science Reports of the Tokyo Bunrika Daigaku (B)* 1 (25): 281-330, pls 17-18 [colour].
- SAKAI T. 1936. — *Crabs of Japan. 66 Plates in Life Colours with Descriptions*. 239 pages, 27 pages [bibliography and index], frontispiece [colour], plates 1-66 [colour]. Tokyo. [Dated 1935, published 1936, see Sakai 1939: 739].
- SAKAI T. 1937. — Studies on the Crabs of Japan, II. Oxystomata. *Science Reports of the Tokyo Bunrika Daigaku (B)* 3 (Supplement no. 2): 67-192.
- SAKAI T. 1940. — Bio-geographic review on the distribution of crabs in Japanese waters. *Records of Oceanographic Works in Japan* 11 (1): 27-63 (supplement 2): 67-192.
- SAKAI T. 1956. — *Crabs*. Edtion 1. Shisei-Shoin, Tokyo: 1-60 [List of Latin names], 1-224 p. [Japanese text], 1-4 [Introduction], 69 figs, 6 pls (two coloured).
- SAKAI T. 1965. — *The Crabs of the Sagami Bay collected by His Majesty the Emperor of Japan*. Maruzen Co., Tokyo, i-xvi + 1-206 p. [English section].
- SAKAI T. 1976. — *Crabs of Japan and the Adjacent Seas*. 3 vols, xxix + 773 p. [English vol.]; 16 p., 251 pls [Plates vol.]; 461 p. [Japanese vol.]. Kodansha Ltd, Tokyo, Japan.
- SAKAI T. 1980. — *Crabs. Their morphology and myth*. Second edition. Tokyo: 1-299, 8 pls. <https://www.biodiversitylibrary.org/bibliography/163328>
- SAKAI T. 1985. — Heike-gani, its prosperity and fossils. *Aquabiology* Tokyo 7 (5): 330-336. (In Japanese: 330-333; in English: 334-336).
- SASAKI J. 2019. — *The Species List of Decapoda, Euphausiacea, and Stomatopoda, all of the World*. Local Independent Administrative Agency Hokkaido Research Organization, Resources Management and Enhancement Division, (Dôsôken) Abashiri Fisheries Research Institute, Fisheries Research Department: 1-14644.
- SCHUBART C. D. & NG P. K. L. 2020. — Revision of the intertidal and semiterrestrial crab genera *Chirromantes* Gistel, 1848, and *Pseudosesarma* Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae), using morphology and molecular phylogenetics, with the establishment of nine new genera and two new species. *Raffles Bulletin of Zoology* 68: 891-994. <https://doi.org/10.26107/RBZ-2020-0097>
- SERÈNE R. 1937. — Inventaire des invertébrés marins de l'Indochine (1^{re} Liste). *Institut Océanographique de l'Indochine* 30: 1-84.
- SERÈNE R. 1968. — The Brachyura of the Indo-West Pacific region, in *Prodromus for a check list of the non-planctonic marine fauna of South East Asia*. Singapore National Academy of Sciences, Special publication No. 1, Fauna IIIC3: 33-112.
- SERÈNE R. & ROMIMOHTARTO K. 1969. — Observations on the species of *Dorippe* from the Indo-Malayan Region. *Marine Research in Indonesia (Penelitian Laut di Indonesia)* 9: 1-35.
- SHEN C.-J. 1931. — The Crabs of Hong Kong, Part 1. *Hong Kong Naturalist* 2 (2): 92-110.
- SHEN C.-J. 1932. — The Brachyuran Crustacea of North China. *Zoologica Sinica (A)* 9 (1): i-x, 1-320, pls 1-10.
- SHEN C. J. 1937a. — On some account of the crabs of North China. *Bulletin of the Fan Memoria Institute of Biology (Zoology)* Peiping 7 (5): 167-185.

- SHEN C.-J. 1937b. — Second Addition to the fauna of brachyuran Crustacea of North China, with a check list of the species recorded in this particular region. *Contributions from the Institute of Zoology, National Academy of Peiping* 3 (6): 277-312.
- SHEN C.-J. 1940a. — The Brachyuran Fauna of Hong Kong. *Journal of the Hong Kong Fisheries Research Station* 1 (2): 211-242.
- SHEN C.-J. 1940b. — On the collections of crabs of South China. *Bulletin of the Fan Memorial Institute (Zoology)* 10 (2): 69-104.
- SHEN C.-J. 1948. — On a collection of crabs from the Shantung Peninsula, with notes on some new and rare species. *Contributions from the Institute of Zoology, National Academy of Peiping* 4 (3): 105-118.
- SHEN C. J. & LIU J. Y. 1963. — Preliminary studies on the characteristics of the crab fauna of Chinese seas. *Oceanologia et Limnologia Sinica* 5 (2): 139-153. (In Chinese and English).
- SHIH H.-T., NG P. K. L., WONG K. J. H. & CHAN B. K. K. 2012. — *Gelasimus splendidus* Stimpson, 1858 (Crustacea: Brachyura: Ocypodidae), a valid species of fiddler crab from the northern South China Sea and Taiwan Strait. *Zootaxa* 3490 (1): 30-47. <https://doi.org/10.11646/zootaxa.3490.1.2>
- SIEBOLD G. T. DE [PH. F.] 1824. — *De Historiae naturalis in Japonia statu, nec non de augmento emolumentisque in decursu perscrutationum exspectandis Dissertatio, cui accedunt Spicilegia Faunae Japonicae*. Batavia: 1-16. [Facsimile reprint edition published in Tokyo on 5 June 1937, with an Introduction to Siebold's *De Historiae naturalis in Japonia statu* by T. Esaki: 3 p.]
- SIEBOLD G. T. DE [PH. F.] 1826. — *De Historiae naturalis in Japonia statu nec non de augmento emolumentisque in decursu perscrutationum exspectandis Dissertatio, cui accedunt Spicilegia Faunae Japonicae*. Wirceburgi (= Würzburg, Germany): 1-20. [Facsimile reprint edition published in Tokyo in 1937 together with reprint of previous item]
- SIEBOLD G. T. DE [PH. F.] 1850. — Commentatio physico-historica de Crustaceis Japonicis, in PH. F. VON SIEBOLD, *Fauna Japonica (Crustacea)*: vii-xvii.
- SIN Y. W., LAI J. C. Y., NG P. K. L. & CHU K. H. 2009. — Phylogeny of Dorippoidea (Crustacea: Decapoda: Brachyura) inferred from three mitochondrial genes. *Invertebrate Systematics* 23 (3): 223-230. <https://doi.org/10.1071/IS09020>
- SOARES-SILVA A. C., COUTO E. C. G. & CARVALHO F. L. 2024. — Mouthparts of the crab *Goniopsis cruentata* (Latreille, 1803) (Decapoda, Brachyura, Grapsidae): morphological variations associated with environment, sex and stage of development. *Animal Biology* 74 (1): 1-19. <https://doi.org/10.1163/15707563-bja10121>
- STEBBING T. R. R. 1893. — A history of Crustacea, Recent Malacostraca. *The International Scientific Series* 74: xvii + 466 p. [New York edition, 1893, D. Appleton & Co., is in International Scientific Series, volume 71, with same pagination.] <https://doi.org/10.5962/bhl.title.11269>
- STIMPSON W. 1858. — Crustacea Oxystomata. Prodomus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit, Part VI. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1858: 159-164.
- STIMPSON W. 1907. — Report on the Crustacea (Brachyura and Anomura) collected by the North Pacific Exploring Expedition, 1853-1856. *Smithsonian Miscellaneous Collections* 49: 1-240. <https://doi.org/10.5962/bhl.title.11269>
- SUGANO T. 1981. — *Sea of Ariake - Its Nature, Animals and Plants, with Guide for Observation*. Tohoku University Press, Tokyo. viii + 194 p.
- TAKEDA M. 1975. — Brachyura, in UTINOMI H. (ed.), *The Aquatic Lower Animals of Japan*. Gakken Chukosei Zukan 9: 342 p. [p. 120-149 (figures with Latin names, and indications of characters with arrows), 188-331 (descriptions of the species figured in order of the Japanese names according to the Japanese alphabet). Gakken Co. Ltd, Tokyo. (In Japanese. Second printing in 1976) [Volumes reprinted in 1978, 1982, 1983].
- TAKEDA M. 1982. — *Keys to the Japanese and Foreign Crustaceans fully Illustrated in Colors*. First Edition. Tokyo: i-vi, 1-58 [keys], 1-285. (In Japanese).
- TAKEDA M. 1983. — see Takeda 1975 and 1976.
- TAKEDA M. & UESHIMA R. 2006. — Crabs preserved in the Department of Zoology, the University Museum, the University of Tokyo, in UESHIMA R. (ed.), *Catalogue of Invertebrate Collection Deposited in the Department of Zoology, the University Museum, The University of Tokyo*. The University Museum, the University of Tokyo Material Reports 62: 61-105. (In Japanese with English text). http://umdb.um.u-tokyo.ac.jp/DDoubutub/pdf_mr/MR_062-03.pdf
- TAKEDA M., SAKAI K., SHINOMIYA S. & SUGA H. 2000. — Crabs from the Seto Inland Sea, Southern Japan. *Memoirs of the National Science Museum* 33: 135-144. (In Japanese with English summary).
- TAKEDA M., KOMATSU H., SHIKATANI N., T. MAENOSONO T. & NARUSE T. 2019. — Annotated list of subtidal crabs in the Shikatani Collection made at Nakagusuku Bay, Okinawa Island, the Ryukyu Islands, Japan. *Fauna Ryukyuan* 50: 1-69, 20 pls. (In Japanese, with English abstract and figure captions).
- TAKEDA M., KOMAI T., KOMATSU H. & IKEDA H. 2006. — Crab fauna of the Sagami Sea, Pacific coast of central Japan, in *Study on environmental changes in the Sagami Sea and adjacent coastal area with time serial comparison of fauna and flora*. II. Marine organisms (animals [Arthropods-Chordates]). *Memoirs of the National Science Museum* (41): 183-215. (In Japanese with English abstract).
- TAKEDA M., FURUTA S., MIYANAGA T., TAMURA A. & WADA T. 2011. — Crabs from the southwestern Sea of Japan along Tottori Prefecture and its vicinity, Japan. *Bulletin of the Tottori Prefectural Museum* 48: 29-94. (In Japanese with English abstract).
- TAKIGAWA Y. 2017. — History of biology studied by western scientists during Edo Period, with remarks on Seto Inland Sea. *Nara Prefectural University kenkyu kiho quarterly review* 27 (3): 93-117. (In Japanese).
- TAKOSHIMA S. 2016. — People who turned into crabs (4). *Transactions of the Institute for Cultural Studies, Aichi Gakuin University, Ningen Bunka* 31: 41-55. (In Japanese).
- TAMURA K., STECHER G. & KUMAR S. 2021. — MEGA11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution* 38 (7): 3022-3027. <https://doi.org/10.1093/MOLBEV/MSAB120>
- TERADA M. 1981. — Zoel development of three species of crab in the subfamily Dorippinae. *Zoological Magazine (Tokyo)* 90: 21-32.
- TERAZAKI T. 1902. — Nippon Kanirui-Tsusetu [= On the Crabs of Japan] 3. *Zoological Magazine* 14 (161): 83-90. (In Japanese).
- UMEMOTO M. & H. KARASAWA H. 1998. — Decapod crustaceans from the Holocene Nanyo Formation of Aichi Prefecture, Japan. *Kasekinotomo* 45: 10-19.
- URITA T. 1918. — List of crabs from Kagoshima Prefecture. *Zoological Magazine (Tokyo)* 30 (354) part I: 160-164.
- URITA T. 1926. — A check-list of Brachyura found in Kagoshima Prefecture, Japan. *The Tshingtao Times*: i-iii, 1-41, 1 map.
- VEHOF J. 2020. — *Evolution of sperm storage organs in the early diverging lineage of eubrachyuran Dorippidae (Brachyura, Decapoda)*. Unpublished Doctoral thesis, Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin, 109 p.
- WADA K. 1995. — Brachyura, in NISHIMURA S. (ed.), *Guide to seashore animals of Japan with color pictures and keys*. Vol. 2: 379-418, pls 101-118. (In Japanese).
- WANG T.-W., CHAN T.-Y. & CHAN B. K. K. 2013a. — Diversity and community structure of decapod crustaceans at hydrothermal vents and nearby deep-water fishing grounds off Kueishan Island, Taiwan: a high biodiversity deep-sea area in the NW Pacific. *Bulletin of Marine Science* 89 (2): 505-528.
- WANG T.-W., CHAN T.-Y., HUANG C.-W. & CHAN B. K. K. 2013b. — Thirty years of changes in the decapod community from the deep water fishing grounds off Kueishan Island, Taiwan,

- Crustaceana* 86 (11): 1382-1409. <https://doi.org/10.1163/15685403-00003218>
- WANG T.-W., KUO P.-H., LIN C.-W., HUANG C.-W., CHAN T.-Y. & CHAN B. K. K. 2017. — Assessing the biodiversity of deep-sea large crustaceans through fishing ports. *Journal of Crustacean Biology* 37 (4): 490-495. <https://doi.org/10.1093/jcabiol/rux044>
- WINDSOR A. M. & FELDER D. L. 2014. — Molecular phylogenetics and taxonomic reanalysis of the family Mithracidae MacLeay (Decapoda: Brachyura: Majoidea). *Invertebrate Systematics* 28 (2): 145-173 <https://doi.org/10.1071/IS13011>
- WONG K. J. H., TAO L. S. R. & LEUNG K. M. Y. 2021. — Subtidal crabs of Hong Kong: Brachyura (Crustacea: Decapoda) from benthic trawl surveys conducted by the University of Hong Kong, 2012 to 2018. *Regional Studies in Marine Science* 48: 102013. <https://doi.org/https://doi.org/10.1016/j.rsma.2021.102013>
- WU Q., LI Z., DAI F., CHEN R., WANG J., SHAN X. & JIN X. 2016. — Taxonomic diversity of crustaceans in Yellow Sea and Bohai Sea. *Biodiversity Science* 24 (11): 1306-1314. (In Japanese and English).
- YAMAGUCHI T. & BABA K. 1993. — Crustacean specimens collected in Japan by Ph. F. Von Siebold and H. Bürger and Held by the Nationaal Natuurhistorisch Museum in Leiden and Other Museums, in YAMAGUCHI T. (ed.), *Ph. F. von Siebold and Natural History of Japan. Crustacea*. The Carcinological Society of Japan. Shimoda Printing, Kumamoto: 145-570, figs 1-200-D + IIA-F + 3 fig. n.n. + IIIA-D.
- YAMAGUCHI T. & HOLTHUIS L. B. 2001. — *Kai-ka Rui Siya-sin*, a collection of pictures of crabs and shrimps, donated by Kurimoto Suiken to Ph. F. von Siebold. *Calanus (Bulletin of the Aitsu Marine Biological Station, Kumamoto University)* Special Number 3: 1-156.
- YAMAGUCHI T., TAKEDA M. & TOKUDOME K. 1976. — A list of crabs collected in the vicinity of the Aitsu Marine Biological Station and a preliminary report on the cheliped asymmetry of the crabs. *Calanus (Bulletin of the Aitsu Marine Biological Station, Kumamoto University)* 5: 31-46.
- YAMAGUCHI T., HARADA K., TAKEDA M. & KIKUCHI T. 1987. — Crab Fauna of the Amakusa Islands. *Calanus* 10: 1-71.
- YANG C. M. 1979. — *A List of the Brachyura in the Zoological Reference Collection of the Department of Zoology, University of Singapore*. Department of Zoology, University of Singapore, Guide number 14: viii + 60 p. [Mimeographed].
- YANG S. L. 1986. — The diagnostic value of gastric mill's construction as taxonomic character on the classification of crabs (Brachyura: Crustacea). *Acta Zootaxonomica Sinica* 11 (2): 151-159. (In Chinese).
- YOKOYA Y. 1933. — On the distribution of Decapod Crustaceans inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S.S. Sôyô-Marû, during the years 1923-1930. *Journal of the College of Agriculture, Tokyo Imperial University* 12 (1): 1-226.
- ZHOU N. Q. & SUN L. C. 1986. — Preliminary report on a survey of brachyuran crustacea from the coast of Liaoning Province, China. *Transactions of the Chinese Crustacean Society* 1: 223-226.
- ZIMMERMANN G., BOSCH P., VALADE P., CORNETTE R., AMÉZIANE N. & DEBAT V. 2012. — Geometric morphometrics of carapace of *Macrobrachium australe* (Crustacea: Palaemonidae) from Reunion Island. *Acta Zoologica* 93 (4): 492-500. <https://doi.org/10.1111/j.1463-6395.2011.00524.x>

Submitted on 12 March 2024;
accepted 18 May 2024;
published on 10 December 2024.