RESEARCH ARTICLE

JOURNAL OF morphology WILEY

Morphology of the gastric mill teeth in dotillid crabs (Crustacea: Brachyura: Dotillidae) from Indonesia

Dewi C. Murniati[1,2,3] (ORCID) | Akira Asakura[3,4] | Tomoyuki Nakano[3] | Michitaka Shimomura[3]

[1]Research Center for Biosystematics and Evolution, National Research and Innovation Agency (BRIN), Bogor, Indonesia

[2]Department of Zoology, Biological Science, Graduate School of Science, Kyoto University, Kyoto, Japan

[3]Seto Marine Biological Laboratory, Field Science Education and Research Center, Kyoto University, Wakayama, Japan

[4]Field Science Education and Research Center, Kyoto University, Kyoto, Japan

Correspondence
Dewi C. Murniati, Research Center for Biosystematics and Evolution, National Research and Innovation Agency (BRIN), Jl. Raya Jakarta Bogor KM 46, Cibinong, 16911, Bogor, Indonesia.
Email: dewicitramurniati@gmail.com

Funding information
Indonesia Endowment Fund for Education (Lembaga Pengelola Dana Pendidikan-LPDP), The Ministry of Finance of the Republic of Indonesia

Abstract

The gastric mill is a prominent structure in the digestive system of brachyuran crabs, consisting of a median tooth plate and a pair of lateral tooth plates. Among crab species that are deposit feeders, the morphology and size of the gastric mill teeth are correlated with the preferred substrate types and food spectrum. In this study, we provide a detailed description of the morphology of the median and lateral teeth of the gastric mills in eight species of dotillid crabs from Indonesia, and compare them in relation to habitat preferences and molecular phylogeny. *Ilyoplax delsmani*, *Ilyoplax orientalis*, and *Ilyoplax strigicarpus* have comparatively simple shapes of their median and lateral teeth, with fewer teeth on each lateral tooth plate compared to *Dotilla myctiroides*, *Dotilla wichmanni*, *Scopimera gordonae*, *Scopimera intermedia*, and *Tmethypocoelis* aff. *ceratophora*, which have more complexly shaped median and lateral teeth, with a greater number of teeth on each lateral tooth plate. The number of teeth on lateral tooth correlates with habitat preference, that is, dotillid crabs inhabiting muddy substrata have fewer teeth on the lateral tooth plate, and those inhabiting sandy substrata have a more teeth. Phylogenetic analysis using partial COI and 16S rRNA genes supports that teeth morphology is similar among closely related species. Therefore, the description of median and lateral teeth of the gastric mill is expected to contribute to the systematic study of dotillid crabs.

KEYWORDS
16S rRNA, COI, deposit feeder crabs, lateral tooth plate, median tooth plate, phylogeny, propyloric ossicle

1 | INTRODUCTION

Deposit-feeding crabs, such as fiddler crabs and dotillid crabs, feed on particulate organic matter in substrates derived from decomposed organic materials, vascular plants, microalgae, bacteria, and small interstitial organisms (Allen, 2010; Davie et al., 2015). In mudflats and sand flats, various species of deposit-feeding dotillid crabs can be found, with some species inhabiting sand substrates (Gherardi et al., 2002; Lee & Lim, 2004; Takagi et al., 2010), some inhabiting mud substrates (Kitaura & Wada, 2006; Trivedi et al., 2015), and

others inhabiting sandy mud substrates (Trivedi & Vachhrajani, 2018). The morphology of the feeding apparatus in these crabs, including the chelipeds, mouthpart appendages, and gastric mills, is related to the structure of sediment composition in the substrate in which they live.

Milne Edward (1834) was the first referring to a digestive organ called the *stomacale*, or stomach. This organ, referred to as the *cardiacalmagens*, was later described in detail by Nauck (1880, fig. 1) as consisting of the *mittleres superomedianum* (median tooth plate) and the *mittleres superolaterale* (lateral tooth plate). Huxley (1884, fig. 9) introduced the term "gastric mill" for these median and lateral tooth plates, which function in grinding food particles.

The morphology of the gastric mill is often considered species-specific (Allardyce & Linton, 2010; Brösing, 2010; Carvalho et al., 2018; Naderloo et al., 2010) and sometimes used for the purpose of distinguishing between families, genera, species including even cryptic species (Brösing, 2010; Brösing et al., 2007; Felgenhauer & Abele, 1989; Naderloo et al., 2010; Shih, 2015). Therefore, it may be reflected by crab's phylogeny in addition to their feeding ecology.

Among deposit feeders, various anatomy and sizes of gastric mills are known to be related to the preferred substrate types and food spectrum. Icely and Jones (1978) stated that differences in gastric mill morphology among four coexisting species of fiddler crabs resulted from adaptation to feed on a specific type of sediment. Allardyce and Linton (2010) described the morphology of gastric mill and mechanism of the food process in gastric mill of carnivorous, omnivorous, and herbivorous land crabs. They found that the morphology of teeth of the gastric mill is definitely correlated to the type of the food. In addition, Brösing (2010) described the morphology of gastric teeth of some brachyuran crab families. As such, we hypothesize that the teeth morphology correlates with the type of substrata.

The value of morphology of gastric mills for systematic studies is debated. Huang et al. (1998) described the morphology of gastric mill teeth to distinguish between two closely related species, *Ocypode cordimanus* and *Ocypode sinensis*. Sakai et al. (2006) described the morphology of the median and lateral teeth of the *Helice/Chasmagnathus* complex (Varunidae) and claimed that this morphology was useful for distinguishing genera. However, Sakai and Türkay (2013) found in their revisional study of the genus *Ocypode* that gastric mill teeth characteristically varied within species from different localities and were not useful for separating species. Davie et al. (2015) claimed that these teeth were generally not useful in distinguishing closely related species. However, the morphology of teeth of the gastric mill of dotillid crabs, as deposit feeder, has never been studied. Therefore, this study aims to test the possible relationship between morphology of the gastric mill, feeding ecology, and phylogeny.

The primary purpose of this study is to describe the gastric mills of eight species of dotillid crabs commonly found in the Indonesian water. We further test the hypothesis whether the morphology of the gastric mills relates more closely to the feeding ecology of the species, their phylogenic relationship or both. For this purpose, we compare habitats of those crabs and also construct a phylogenetic tree using partial COI and 16S rRNA genes and map morphological features of the gastric mills onto the tree.

2 | MATERIALS AND METHODS

2.1 | Material collection

Eight species of dotillid crabs were used, that is, *Dotilla myctiroides* (Milne Edwards, 1852), *Dotilla wichmanni* (De Man, 1892), *Ilyoplax delsmani* (De Man, 1926), *Ilyoplax orientalis* (De Man, 1888), *Ilyoplax strigicarpus* (Davie, 1990), *Scopimera gordonae* (Serène & Moosa, 1981), *Scopimera intermedia* (Balss, 1934), and *Tmethypocoelis* aff. *ceratophora* (Koelbel, 1897). We use male and female specimens of various size of carapace (carapace width and length) to evaluate intraspecific variation (Table 1).

Some specimens were recently collected from various intertidal areas in Indonesia, including Pariaman Mangrove, Apar, North Pariaman, Pariaman, West Sumatera; Penajam, East Kalimantan; Tosale, Banawa District, Donggala, Central Sulawesi; Tasikoki Beach, Tanjung Merah, Bitung, North Sulawesi; Pancer Mangrove Forest, Serang, Banten; Yasa River, Cilacap, Central Java; Cupek Estuarine, Pamenang, North Lombok; Keakwa, Mimika, Papua (Figure 1). The substrates of the habitats of each species were recorded and classified as sand, muddy, or sandy mud (Table 1).

In addition, we studied some specimens from reference collections in the Museum Zoologicum Bogoriense (MZB) (Figure 1). All collected specimens were preserved in 90% ethanol and deposited in the MZB of the Directorate of Scientific Collection Management, National Research and Innovation Agency (Badan Riset dan Inovasi Nasional-BRIN), Cibinong, Indonesia. Detailed examinations of the morphology were conducted at the Research Center for Biosystematics and Evolution, BRIN, Cibinong, Indonesia.

2.2 | Preparation of gastric mill

Foreguts were removed from the bodies of the crabs, then gastric mills were removed from the foreguts, and their muscle tissues were carefully removed using micro dissecting needles. Lateral and median teeth were separated using micro dissecting needles as well, and the particles inside were collected for observation and classified as hard particle (HP) and soft particle (SP). The teeth were fixed in glutaraldehyde and cacodylate buffer for 24 and 4 h, respectively. They were then dehydrated in several steps of ethanol (50%, 70%, 85%, 90%, 100%), and vacuum-dried using a TITEC VC-96N for 10 min. Each prepared

TABLE 1 Examined materials deposited in Museum Zoologicum Bogoriense (MZB).

Species	Locality; collector	Substrate type	Catalog number; number of samples	Sample size (CW × CL) (mm)
Dotilla myctiroides Milne Edwards (1852)	Lubuk Damar, Aceh Tamiang, Aceh, 98°15′27.16″E 4°17′38.73″S; Damarini A. S.	Sandy	MZB.Cru.5176; 1 male	9.7 × 10.4 (broken carapace)
			MZB.Cru.5176; 1 female	
Dotilla wichmanni De Man (1892)	Depok Beach, Bantul, Yogyakarta; Murniati D. C.	Sandy	MZB.Cru.5125; 3 males	5.4 × 4.2–7.3 × 5.6
	Yasa River, Cilacap, Central Java, 7°44′28.7″S 109°00′36.2″ E; Murniati D. C.		MZB.Cru.5131; 3 females	5.7 × 4.4–7.2 × 5.7
Ilyoplax delsmani De Man (1926)	Pancer Mangrove Forest, Serang, Banten, 6°01′32.0″S 106°09′53.8″E; Murniati D. C., Arifin, Rahmansyah B. A., Arif R. A.	Muddy	MZB.Cru.5135; 3 males	4.1 × 3.1–7.4 × 5.0
			MZB.Cru.5135; 3 females	4.6 × 3.2–5.7 × 4.1
Ilyoplax orientalis (De Man [1888] [in De Man, 1887–1888])	Pancer Mangrove, Serang, Banten, 6°01′32.0″S 106°09′53.8″E; Murniati D. C., Arifin, Rahmansyah B. A., Arif R. A.	Muddy	MZB.Cru.5134; 3 males	7.0 × 3.1–6.5 × 4.5
			MZB.Cru.5137; 1 female	4.9 × 3.1
Ilyoplax strigicarpus Davie (1990)	Yasa River (estuarine), Cilacap, Central Java, 7°44′25.5″S 109°00′39.0″E, coll. D. C. Murniati	Muddy	MZB.Cru.5132; 2 females	5.3 × 3.3–7.3 × 4.4
	Pariaman Mangroves, Apar, North Pariaman, Pariaman, West Sumatera, 0°36′01.1″S, 100°06′35.0″E; Tasya L., Pangestu M. Q., Putra R. M., Salsabyla I., Muchlisin I.		MZB.Cru.5179; 3 males	4.8 × 3.2–5.3 × 3.3
Scopimera gordonae Serène and Moosa (1981)	Keakwa, Mimika, Papua, 04°46′22.63″S, 136°32′02.52″E; Surbakti S.	Sandy	MZB.Cru.5184; 1 male	9.2 × 7.1
Scopimera intermedia Balss (1934)	Tasikoki Beach, Tanjung Merah, Bitung, North Sulawesi, 1°23′24.3″N 125°06′02.9″E; Murniati D. C., Nurdiansyah D.	Sandy	MZB. Cru.5139; 3 females	5.1 × 3.9–5.6 × 4.4
			MZB.Cru.5185; 2 males	4.4 × 3.2–5.7 × 4.5
Tmethypocoelis aff. *ceratophora* Koelbel (1897)	Cupek Estuarine, Pamenang, North Lombok, 8°23′16.8″S 116°06′02.2″E; Anggorowati D. A.	Sandy-mud	MZB.Cru.5117; 3 males	7.1 × 4.0–7.2 × 4.1
			MZB.Cru.5117; 3 females	4.0 × 2.5–4.5 × 2.8

sample was mounted on a specimen stub and coated with gold at 5–8 mA for 5 min using an ion coater (Dewi & Purwaningsih, 2020).

Detailed photographs of the teeth plates of the gastric mills were captured using scanning electron microscopy (SEM), JEOL JSM-IT 200, at an accelerating voltage of 5 kV. The photographs are shown in an inverted position, with the posterior portion at the top. For the median tooth, the widest and longest parts of the propyloric ossicle and the posteromedian-urocardiac ossicle were measured, based on the photograph, using ImageJ software. The size ratio of each part of
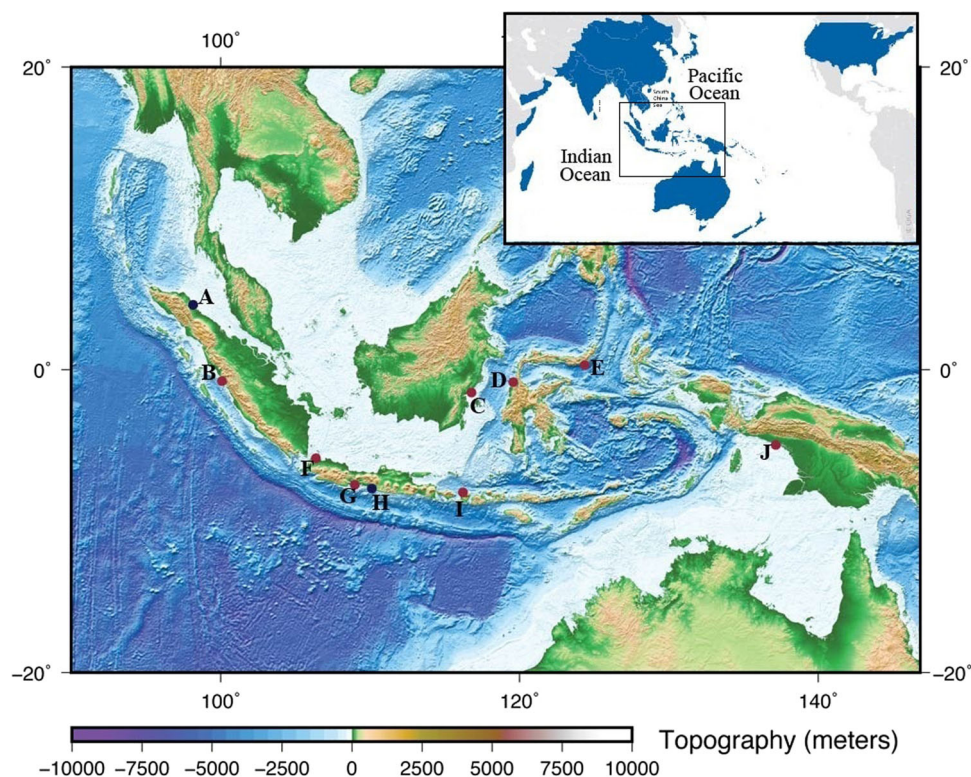
FIGURE 1 Map of the collected specimens. ● Reference collection from MZB, ● recently collected specimen. (A) Lubuk Damar, Aceh Tamiang, Aceh. (B) Pariaman Mangroves, Apar, North Pariaman, Pariaman, West Sumatera. (C) Penajam, East Kalimantan. (D) Tosale, Banawa District, Donggala, Central Sulawesi. (E) Tasikoki Beach, Tanjung Merah, Bitung, North Sulawesi. (F) Pancer Mangrove Forest, Serang, Banten. (G) Yasa River, Cilacap, Central Java. (H) Depok Beach, Bantul, Yogyakarta. (I) Cupek Estuarine, Pamenang, North Lombok. (J) Keakwa, Mimika, Papua (derived from Camroux & Jaffrelot, 2021; Kindpng, 2010). MZB, Museum Zoologicum Bogoriense.

the median tooth was calculated as width/length. Morphological terminology for the teeth of the gastric mill follows Davie et al. (2015) and Lima-Gomes et al. (2017) (Figure 2).

2.3 | Molecular phylogenetic analysis

2.3.1 | Samples, DNA extraction, amplification, and sequencing

Eight species, with three to five samples per species, were used. The muscle tissue was taken from pereopod 5 (P5). For small specimens, one eyestalk from each sample was added to the muscle tissue sample. Each of the collected tissues was placed in a 1.5 mL microtube.

Total DNA from the tissue was isolated using Roche High Pure polymerase chain reaction (PCR) template Preparation kit following the manufacturer's protocol. A partial COI and 16S rRNA genes were selected for amplification with PCR using primers (Table 2). The PCR conditions for the above primers were denaturation for 50 s at 94°C, annealing for 70 s at 45–50°C, and extension for 60 s at 72°C (40 cycles), followed by extension for 10 min at 72°C. The PCR products were sent to 1st Base for sequencing. The company used the Cycle Sequencing Kit Chemistry BidDye® Terminator V3.1 for de novo sequencing, resequencing, and finishing PCR products.

2.4 | Sequence alignment and phylogenetic analysis

Forward and reverse sequences were aligned for the construction of a consensus with MEGA-X, with *Austruca annulipes*, *Austruca perplexa*, and *Ocypode ceratophthalmus* as the outgroups. The analysis was conducted based on an alignment of ~613 bp of COI and 550 bp of 16S. Maximum likelihood (ML) analysis with Kimura-2 parameter was employed to construct the phylogenetic tree. The 10,000 replicates bootstrap method was used to assess the internal consistency the phylogenetic tree branches. Genetic distances were calculated based on CO1 and 16S rRNA sequences separately. A phylogenetic tree with posterior probability was also constructed using MrBayes to confirm the ML phylogenetic tree. The best fitting-model was calculated using JModeltest (Dariba et al., 2012). The Bayesian analysis was conducted using the Monte Carlo Marcov Chain (mcmc) method, with the number of generation (ngen) being 1×10^6 and sample frequency (samplefreq) being 500.
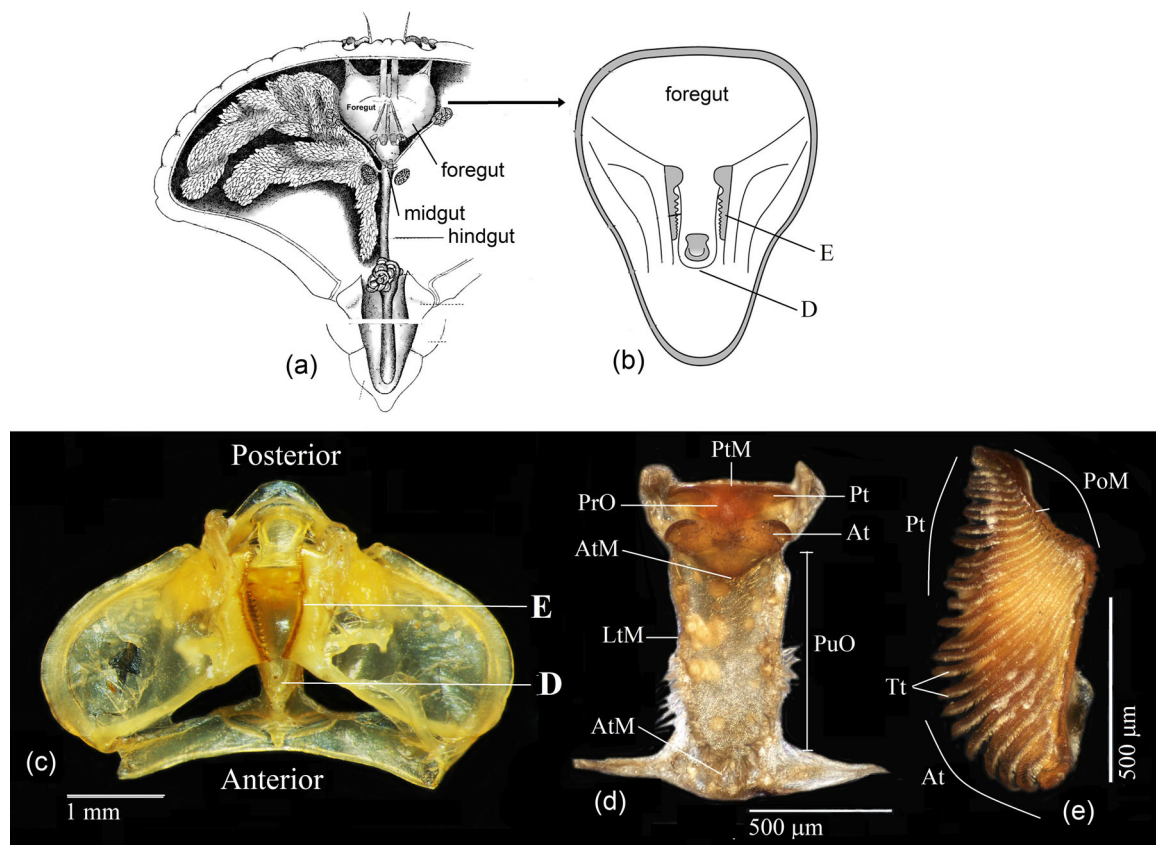
FIGURE 2 Gastric mill and teeth of dotillid crabs. (a) Digestive organ (b) foregut (c) gastric mill (d) median tooth plate, with propyloric ossicle (PrO), posterior tooth (Pt), anterior tooth (At), posterior margin (PtM), anterior margin (AtM), and posteromedian-urocardiac ossicle (PuO) with anterior margin (AtM), lateral margin (LtM) (e) Lateral tooth plate, with teeth (Tt), posterior teeth (Pt), anterior teeth (At), and postero-outer margin (PoM) *Source*: Upper figures are adopted from Davie et al., 2015.

TABLE 2 Primers used for amplification of 16S rRNA and *C* cytochrome oxidase subunit I (COI) by means of polymerase chain reaction (PCR).

Gene	Primer	Sequence	References
16S rRNA	1471	5′-CCTGTTTANCAAAAACAT-3′	Shih et al. (2009)
	1472	5′-AGATAGAAACCAACCTGG-3′	Shih et al. (2010)
CO1	LCO1490	5′-GGTCAACAAATCATAAAGATATTGG-3′	Folmer et al. (1994)
	HCO2198	5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	Folmer et al. (1994)

3 | RESULTS

3.1 | Description of gastric mill

Based on our observation, there are five different shapes of propyloric ossicle in dotillid crabs, that is, ovate, hexagonal, triangular, half-circular, and trapezoid (Figure 3).

3.2 | *D. myctiroides* (Milne Edwards, 1852)

Median tooth plate (Figure 4a). Propyloric ossicle ovate, wider than posteromedian-urocardiac ossicle; size ratio 2.5–2.6; surface slightly convex; complex structure, consisting of two teeth

separated by wide groove, anterior tooth larger than posterior tooth; anterior margin nearly straight; posterior margin straight. Posteromedian-urocardiac ossicle triangular, size ratio 0.5–0.6, length 3.8 times as long as propyloric ossicle; anterior margin pointed; posterior portion wider than anterior portion; lateral margins tubercular on 3/4 of its total length anteriorly, ½ length of lateral margins covered by short setae anteriorly.

Lateral tooth plate (Figure 5a). Consisting of 20–24 slender teeth, each tooth with comb shaped lamellae facing anteriorly, setae short; median teeth 6–7 longest, posterior tooth shortest, postero-outer margin with 9 blunt teeth.

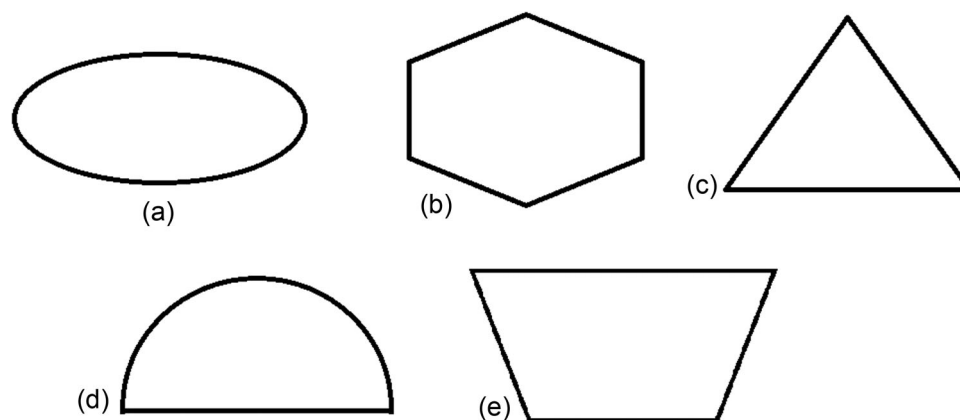*Particles inside gastric mill*. Consist of hard and soft particles (Figure 6a).

FIGURE 3 Schematic shape of propyloric ossicle of median tooth plae. (a) Ovate, (b) hexagonal, (c) triangular, (d) half circular, and (e) trapezoid.
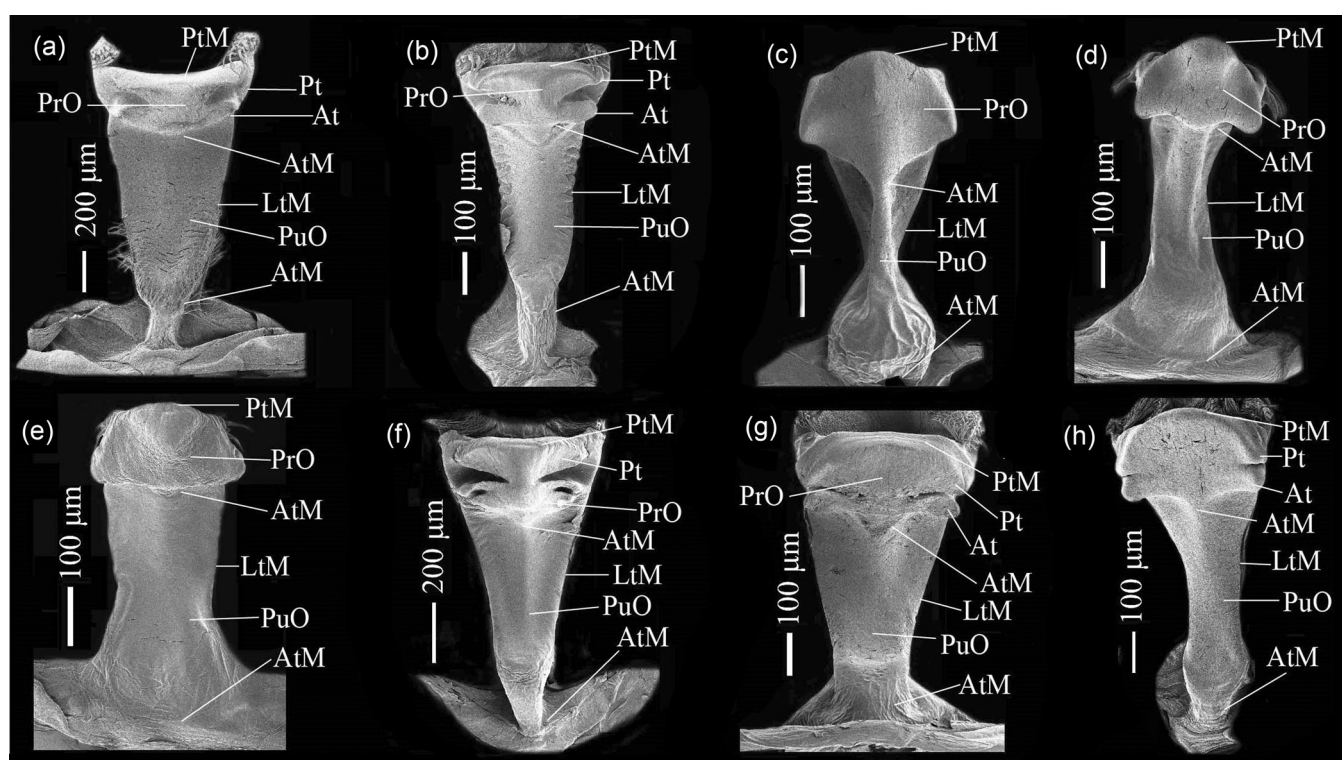

FIGURE 4 Median tooth plate. (a) *Dotilla myctiroides*, male (9.7 × 10.4 mm) (MZB.Cru.5176), Lubuk Damar, Aceh Tamiang, Aceh. (b) *Dotilla wichmanni*, male (7.4 × 5.6 mm) (MZB.Cru.5125), Depok beach, Bantul, Yogyakarta. (c) *Ilyoplax delsmani*, male (7.4 × 5.1 mm) (MZB.Cru.5135), Pancer Mangrove Forest, Serang, Banten. (d) *Ilyoplax orientalis*, male (6.5 × 4.5 mm) (MZB.Cru.5134), Pancer Mangrove, Serang, Banten. (e) *Ilyoplax strigicarpus*, male (4.8 × 3.2 mm) (MZB.Cru.5179), Pariaman Mangroves, Apar, North Pariaman, Pariaman, West Sumatera. (f) *Scopimera gordonae*, male (broken carapace), Keakwa, Mimika, Papua. (g) *Scopimera intermedia*, male (5.8 × 4.5 mm) (MZB.Cru.5185), Tosale, Banawa District, Donggala, Central Sulawesi. (h) *Tmethypocoelis* aff. *ceratophora*, male (7.2 × 4.2 mm) (MZB.Cru.5117), Muara Cupek, Pamenang, North Lombok. MZB, Museum Zoologicum Bogoriense.

3.3 | *D. wichmanni* De Man (1892)

Median tooth plate (Figure 4b). Propyloric ossicle ovate, wider than posteromedian-urocardiac ossicle; size ratio 2.3; surface convex medially; complex structure, consisting of two teeth separated by triangular groove, anterior tooth smaller than posterior tooth; anterior margin nearly straight; posterior margin nearly straight. Posteromedian-urocardiac ossicle triangular, size ratio 0.5, length 3.1 times as long as propyloric ossicle, anterior margin triangular, posterior portion wider than anterior portion, lateral margins with finger shaped structure.

Lateral tooth plate (Figure 5b). Consisting of 19 slender teeth; each tooth with comb shape lamellae facing anteriorly; median teeth
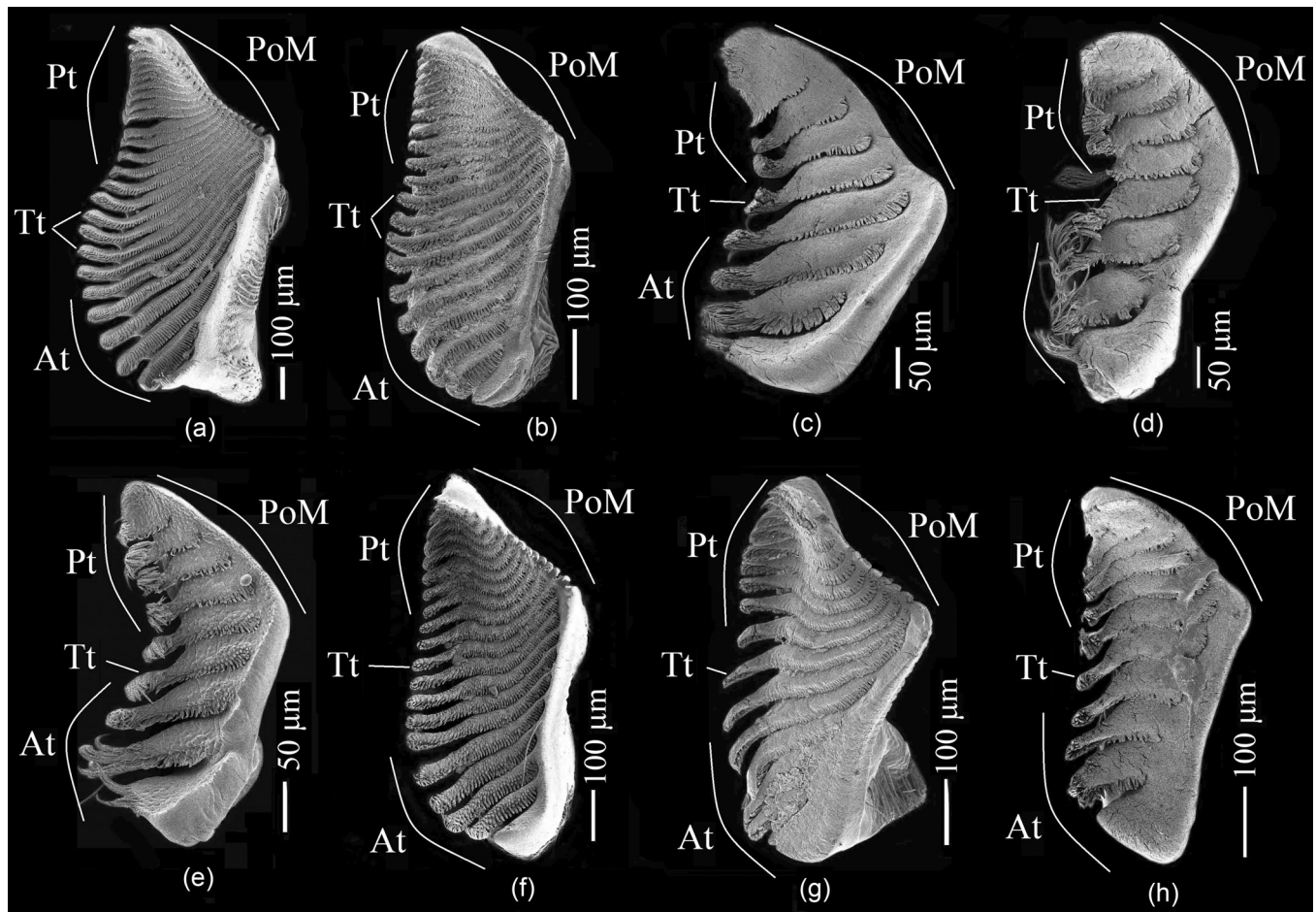
FIGURE 5 Lateral tooth plate. (a) *Dotilla myctiroides*, male (9.7 × 10.4 mm) (MZB.Cru.5176), Lubuk Damar, Aceh Tamiang, Aceh. (b) *Dotilla wichmanni*, male (7.4 × 5.6 mm) (MZB.Cru.5125), Depok beach, Bantul, Yogyakarta. (c) *Ilyoplax delsmani*, male (7.4 × 5.1 mm) (MZB.Cru.5135), Pancer Mangrove Forest, Serang, Banten. (d) *Ilyoplax orientalis*, male (6.5 × 4.5 mm) (MZB.Cru.5134), Pancer Mangrove, Serang, Banten. (e) *Ilyoplax strigicarpus*, male (4.8 × 3.2 mm) (MZB.Cru.5179), Pariaman Mangroves, Apar, North Pariaman, Pariaman, West Sumatera. (f) *Scopimera gordonae*, male (broken carapace), Keakwa, Mimika, Papua. (g) *Scopimera intermedia*, male (5.7 × 4.5 mm) (MZB.Cru.5185), Tosale, Banawa District, Donggala, Central Sulawesi. (h) *Tmethypocoelis* aff. *ceratophora*, male (7.2 × 4.2 mm) (MZB.Cru.5117), Muara Cupek, Pamenang, North Lombok. MZB, Museum Zoologicum Bogoriense.
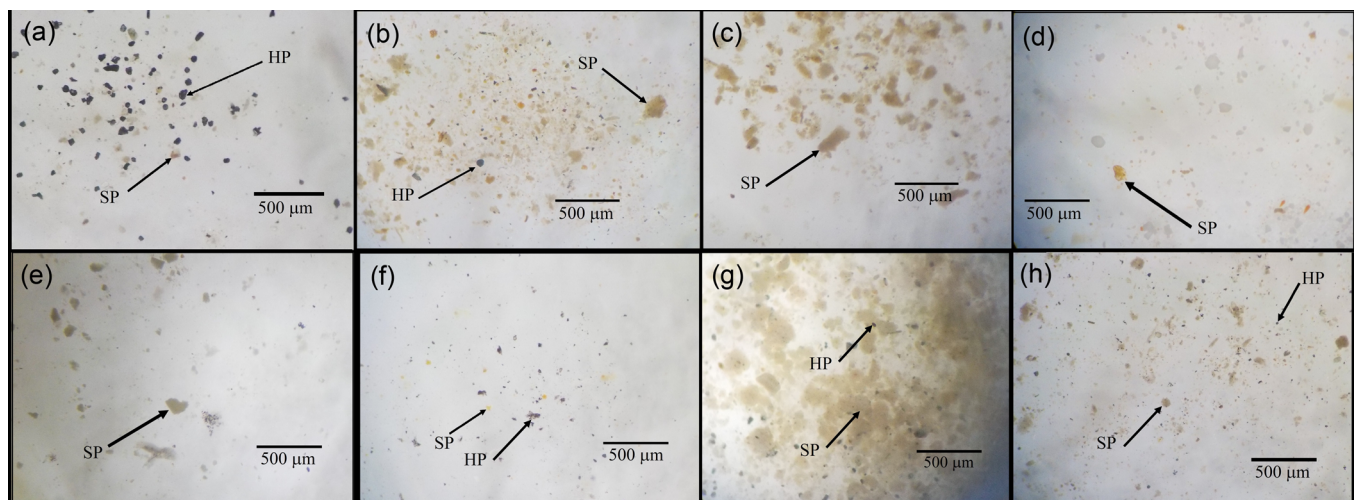

FIGURE 6 Particles collected from gastric mill. (HP) Hard particle (SP) soft particle. (a) *Dotilla myctiroides*, (b) *Dotilla wichmanni*, (c) *Ilyoplax delsmani*, (d) *Ilyoplax orientalis*, (e) *Ilyoplax strigicarpus*, (f) *Scopimera gordonae*, (g) *Scopimera intermedia*, (h) *Tmethypocoelis* aff. *ceratophora*.

7−8 longest, posterior tooth shortest, postero-outer margin with 6 hook-shape teeth.

Particles inside gastric mill. Consist of hard and soft particles (Figure 6b).

3.4 | *I. delsmani* De Man (1926)

Median tooth plate (Figure 4c). Propyloric ossicle nearly hexagonal, wider than posteromedian-urocardiac ossicle; size ratio 1.2; surface convex; simple structure, consisting of one tooth; anterior margin nearly pointed medially; posterior margin convex. Posteromedian-urocardiac ossicle waist-like shape, size ratio 0.5, length 1.6 times as long as propyloric ossicle; anterior margin pointed; posterior portion wider than anterior portion; lateral margins entire.

Lateral tooth plate (Figure 5c). Consisting of six stout teeth, each tooth with row of bristle-like setae anteriorly; third anterior tooth longest, posterior tooth shortest; postero-outer margin without teeth.

Particles inside gastric mill. Consist of SP (Figure 6c).

3.5 | *I. orientalis* (De Man, 1888 [in De Man, 1887–1888])

Median tooth plate (Figure 4d). Propyloric ossicle triangular, wider than posteromedian-urocardiac ossicle; size ratio 1.4, surface convex; simple structure, consisting of one tooth; anterior margin tridentatus; posterior margin arched. Posteromedian-urocardiac ossicle rectangular shape, size ratio 0.3, length 2.5 times as long as propyloric ossicle; anterior margin convex; posterior portion narrower than anterior portion; lateral margins entire, slightly concave medially.

Lateral tooth plate (Figure 5d). Consisting of six stout swollen teeth, each tooth with one row of bristle-like setae anteriorly; first three anterior teeth with nearly similar size; last three posterior teeth equally smaller than first three anterior teeth; postero-outer margin without teeth.

Particles inside gastric mill. Consist of SP (Figure 6d).

3.6 | *I. strigicarpus* Davie (1990)

Median tooth plate (Figure 4e). Propyloric ossicle trapezoid, wider than posteromedian-urocardiac ossicle; size ratio 1.7, surface convex; simple structure, consisting of one tooth; anterior margin straight; posterior margin slightly convex. Posteromedian-urocardiac ossicle rectangular, size ratio 0.5, length 2.6 times as long as propyloric ossicle; posterior portion as wide as anterior portion; anterior margin convex; lateral margins entire, slightly concave medially.

Lateral tooth plate (Figure 5e). Consisting of seven moderate teeth, each tooth with one row of bristle-like setae anteriorly; teeth 1−3 equally long, teeth 1−4 equally shorter than first 3 teeth; upper-outer margin without teeth.

Particles inside gastric mill. Consist of SP (Figure 6e).

3.7 | *S. gordonae* Serène and Moosa (1981)

Median tooth plate (Figure 4f). Propyloric ossicle trapezoid; size ratio 1.9; median surface convex; complex structure, consisting of three teeth; anterior tooth larger than median tooth, separated by narrow gap; posterior tooth larger than anterior tooth, posterior and median teeth separated by wide gap; anterior margin arched; posterior margin nearly straight; lateral margins entire, parallel to lateral margins of posteromedian-urocardiac ossicle. Posteromedian-urocardiac ossicle triangular, size ratio 0.7, length 2.6 times as long as propyloric ossicle; narrow anteriorly, anterior margin convex; wider posteriorly; lateral margins entire.

Lateral tooth plate (Figure 5f). Consisting of 19 teeth, each tooth fully covered with bristle-like setae; anterior teeth 6−8 longest; posterior tooth shortest; postero-outer margin with 9 hook-shaped teeth.

Particles inside gastric mill. Consist of hard and soft particles (Figure 6f).

3.8 | *S. intermedia* Balss (1934)

Median tooth plate (Figure 4g). Propyloric ossicle half circular, wider than posteromedian-urocardiac ossicle; size ratio 1.6; median surface flat; complex structure, consists of two teeth, separated by furrow, anterior tooth smaller than posterior tooth; anterior margin arched; posterior margin convex; lateral margins parallel to posteromedian-urocardiac ossicle. Posteromedian-urocardiac ossicle triangular, size ratio 0.8, length 1.6 times as long as propyloric ossicle; narrow anteriorly, anterior margin convex; wide posteriorly; lateral margins entire.

Lateral tooth plate (Figure 5g). Consisting of 14 teeth, each tooth covered with lamellar setae anteriorly; anterior teeth 5−6 longest; posterior tooth shortest; postero-outer margin with 6 wide teeth.

Particles inside gastric mill. Consist of hard and soft particles (Figure 6g).

3.9 | *T.* aff. *ceratophora* Koelbel (1897)

Median tooth plate (Figure 4h). Propyloric ossicle half circular, wider than posteromedian-urocardiac ossicle; size ratio 1.4; median surface slightly convex; simple structure, slightly consisting of two teeth, separated by lateral truncation, anterior tooth smaller than posterior tooth; anterior margin pointed; posterior margin convex; lateral margins parallel to posteromedian-urocardiac ossicle. Posteromedian-urocardiac ossicle triangular, size ratio 0.7, length 1.7 times as long as propyloric ossicle; narrow anteriorly, anterior margin convex; wide posteriorly; lateral margins entire.

Lateral tooth plate (Figure 5h). Consisting of 9−10 stout teeth, teeth gradually lessen stout posteriorly, each tooth covered with one row of bristle-like setae anteriorly; first anterior tooth swollen, anterior teeth 3−4 longest, posterior tooth shortest; postero-outer margin without teeth.

Particles inside gastric mill. Consist of hard and soft particles (Figure 6h).

3.10 | Intraspecific variation in gastric mill morphology

Within all eight species, no significant morphological differences in gastric mill teeth are observed by size or sex.

3.11 | Interspecific difference in gastric mill morphology

Various interspecific differences were observed in the shapes of lateral tooth plates and propyloric and posteromedian-urocardiac ossicles of the median tooth plate (Figure 3 and Table 3). The shape of the propyloric ossicle varies between species, particularly in the size ratio of length to width and the gap between teeth. For example, *D. myctiroides* has wider propyloric ossicles than *D. wichmanni*, with a wider gap between teeth and a wider anterior tooth than posterior tooth. In *D. wichmanni*, these features are the opposite shape compared to *D. myctiroides*. Among the *Ilyoplax* species, differences are seen in the shape of the propyloric ossicle and posteromedian-urocardiac ossicle. *I. delsmani* and *I. strigicarpus* have a trapezoidal posteromedian-urocardiac ossicle, while *I. orientalis* has a triangular one. Among the *Scopimera* species, there are marked differences in the shape and number of teeth on propyloric ossicles.

Taking all of these characteristics into account, the morphology of the gastric mills of the eight species studied here can be roughly divided into two types. *I. delsmani*, *I. orientalis*, and *I. strigicarpus* have lateral and median teeth of comparatively simpler shape, with a lower number of stout teeth on each lateral tooth plate: 6 teeth in *I. delsmani*, 6 in *I. orientalis*, and 7 in *I. strigicarpus*. The propyloric ossicle of the median tooth of these species consists of only 1 tooth.

On the other hand, *D. myctiroides*, *D. wichmanni*, *S. gordonae*, *S. intermedia*, and *T.* aff. *ceratophora* have lateral and median teeth of a more complex structure, with a larger number of slender teeth on each lateral tooth plate: 20–24 teeth in *D. myctiroides*, 19 in *D. wichmanni*, 19 in *S. gordonae*, 14 in *S. intermedia*, and 9–10 in *T.* aff. *ceratophora*. The propyloric ossicle of the median tooth in these species consists of more than 1 tooth.

3.12 | DNA analysis

The data set consists of 1163 bp from two mitochondrial genes, including 550 bp of the partial 16S gene and 613 bp of the partial COI gene. The best-fit evolution models for concatenated genes in the Bayesian analysis were TPM3uf + I + G and TVM + G. The phylogenetic tree from MEGA-X and Bayes shows similar branches with high posterior probability (Figure 7). In general, there are two main clades in the family. Two species of *Ilyoplax*, *I. orientalis* and *I. strigicarpus*,

form a single clade, all of which have simple teeth of gastric mills. *Scopimera* and *Tmethypocoelis*, which all have complex teeth of gastric mills, are in separate clades. Meanwhile *Dotilla*, which has complex teeth structure, is in the same clade as the genus *Ilyoplax*.

4 | DISCUSSION

In the present study, we provide the first description of the teeth morphology of dotillid crabs. We found that there is no intraspecific variation, indicating that the characteristics of the gastric mill teeth are not affected by the sex or size of the crabs, making this a consistent character within a species and useful as a reliable marker for identifying closely related or cryptic species. However, interspecific differences were found in the morphology of the propyloric ossicle and the number of teeth on the lateral tooth.

These findings are in consensus with those of Shih (2015) and Shih, Ng, et al. (2015), who found that the characteristics of the median tooth plate in the gastric mill, particularly the urocardiac ossicles, are sufficient and useful for distinguishing species. Moreover, variation in the number of teeth on the propyloric ossicles have been detected in the *Austruca lactea* species complex, with numbers ranging from 5 in *A. perplexa* to 8 in *A. albimana* (Naderloo et al., 2010).

4.1 | Relationship between morphology of lateral tooth plate and habitat substrata

Our field observations recorded that *Dotilla* and *Scopimera* species inhabited sandy substrates, *Ilyoplax* species inhabited fine muddy substrates, and *Tmethypocoelis* species inhabited sandy-mud substrates. This suggests that there may be a tendency for species with lateral tooth plates bearing a larger number of teeth to inhabit sandy habitats and those with fewer teeth to inhabit muddy habitats (Table 3). However, the particle size and water content, are not described in the present study.

This finding aligns with the observation by Naderloo et al. (2010) that the *Uca lactea* species group inhabiting sand flats have lateral tooth plates armed with more than 10 teeth. Similarly, Brösing's (2010) SEM photograph of teeth showed that *Mictyris longicarpus*, which inhabits sandy habitats (Rossi & Chapman, 2003), has lateral tooth plates consisting of 23 teeth, and *Gelasimus tetragonon*, which inhabits substrates composed of coarse sand adjacent to coral reefs (Shih et al., 2016), has 22 teeth on its lateral tooth plate.

The cup-like hollow directly behind the anterior teeth of the lateral teeth would function as an effective "pestle" as the "mortar-like" process (propyloric ossicle) of the median tooth is drawn forward. Any food trapped in this hollow would be pulverized by the crushing action of the median tooth (Allardyce & Linton, 2010).

Dotilla and *Scopimera* scrape and intake the organic materials from sand particles, and *Tmethypocoelis* scrapes and intake organic materials from sandy-mud particles. Some sand particles potentially

TABLE 3 Morphological comparison of median and lateral teeth plate of the gastric mill on dotillid crabs on the basis of substrate types.

	Dotilla myctiroides	*Dotilla wichmanni*	*Ilyoplax delsmani*	*Ilyoplax orientalis*	*Ilyoplax strigicarpus*	*Scopimera gordonae*	*Scopimera intermedia*	*Tmethypocoelis aff. ceratophora*
Occupied substrate	Sandy	Sandy	Muddy	Muddy	Muddy	Sandy	Sandy	Sandy-mud
Particles inside gastric mill								
• Hard	+	+	-	-	-	+	+	+
• Soft	+	+	+	+	+	+	+	+
A. Median tooth plate								
• Propyloric ossicle								
Shape	Ovate	Ovate	Trapezoid	Triangular	Trapezoid	Trapezoid	Half circular	Half circular
Size ratio (length/width)	2.5–2.6	2.3	1.2	1.4	1.7	1.9	1.6	1.4
Structure, number of teeth	Complex shape, two teeth	Complex shape, two teeth	Simple shape, one tooth	Simple shape, one tooth	Simple shape, one tooth	Complex shape, three teeth	Complex shape, two teeth	Simple shape, slightly two teeth
Anterior margin	Nearly straight	Nearly straight	Nearly pointed medially	Tridentatus	Straight	Arched	Arched	Pointed
Posterior margin	Straight	Nearly straight	Convex	Arched	Slightly convex	Nearly straight	Convex	Convex
• Posteromedian–urocardiac ossicle								
Shape	Triangular	Triangular	Waist-like shape	Rectangular	Rectangular	Triangular	Triangular	Triangular
Size ratio (length/width)	0.5–0.6	0.5	0.5	0.3	0.5	0.7	0.8	0.7
Length	3.8 times as long as propyloric ossicle	3.1 times as long as propyloric ossicle	1.6 times as long as propyloric ossicle	2.5 times as long as propyloric ossicle	2.6 times as long as propyloric ossicle	2.6 times as long as propyloric ossicle	1.6 times as long as propyloric ossicle	1.7 times as long as propyloric ossicle
Anterior margin	Pointed	Triangular	Pointed	Convex	Convex	Convex	Convex	Convex
Posterior portion	Wider than anterior portion	Wider than anterior portion	Wider than anterior portion	Narrower than anterior portion	As wide as anterior portion	Wider than anterior portion	Wider than anterior portion	Wider than anterior portion
Lateral margin	Tubercular on 3/4 of its total length anteriorly, 1/2 length of lateral margins covered by short setae anteriorly	With finger shaped structure	Entire	Entire, slightly concave medially	Entire, slightly concave medially	Entire	Entire	Entire

TABLE 3 (Continued)

	Dotilla myctiroides	Dotilla wichmanni	Ilyoplax delsmani	Ilyoplax orientalis	Ilyoplax strigicarpus	Scopimera gordonae	Scopimera intermedia	Tmethypocoelis aff. ceratophora
B. Lateral tooth plate								
Number of teeth	20–24 slender teeth	19 slender teeth	6 stout teeth	6 stout swollen teeth	7 moderate teeth	19 slender teeth	14 slender teeth	9–10 stout teeth
Longest teeth	Median teeth 6–7	Median teeth 7–8	Third anterior tooth	-	-	Anterior teeth 6–8	Anterior teeth 5–6	Anterior teeth 3–4
Shortest tooth	Posterior tooth	Posterior tooth	Posterior tooth	-	-	Posterior tooth	Posterior tooth	Posterior tooth
Postero-outer margin	With 9 blunt teeth	With 6 hook-shape teeth	Without teeth	Without teeth	Without teeth	With 9 hook-shaped teeth	With 6 wide teeth	Without teeth

included in the intake and subsequently transported into gastric mill (Figure 6a,b,f–h). Consequently, the gastric mill would require an efficient "mortar and pestle" system to crush and grind these HP. The presence of the teeth features of the gastric mill is closely linked to the process of fragmenting sand material. As sand enters the stomach as HP, the initial anterior teeth of the lateral tooth plate perform the grinding action, while the postero-outer teeth of the two lateral teeth contribute to further crush the ingested food fragments. Simultaneously, as the median tooth is drawn forward during the "grinding" mode of chewing, food is ground between the surface of the two lateral teeth and the head of the median tooth.

In contrast, *Ilyoplax* species primarily intake organic materials from mud, hence SP are dominant inside the gastric mill (Figure 6c–e). Therefore, the teeth are more specialized for crushing soft food particles. The median tooth of *Ilyoplax* is simple, making it well-suited for crushing soft items. It consists of a "blunt" propyloric ossicle and a smooth, sole-like plate. This structure aligns well with the teeth along the lateral teeth, so that any food items trapped in the mill are ground as the teeth move past each other during the grinding and crushing chewing process.

The simple structure of propyloric ossicle was exemplified by carnivorous grapsid crabs (Allardyce & Linton, 2010). Their gastric mill was well-suited for pulverizing soft animal material. The median tooth possessed a large, rounded, and blunt propyloric ossicle (referred to as the posterior process), which in vivo would fit into the flattened grooves of the lateral teeth and function as a mortar and pestle. In contrast, the median and lateral teeth of herbivorous gecarcinids were sharper, respectively possessing well-defined teeth (referred to as ridges) on the propyloric ossicle and postero-outer teeth (referred to as cusps). In vivo, these interlocking propyloric ossicle and postero-outer teeth would form effective cutting surfaces, making the gastric mill of herbivores well-suited for processing a hard and fibrous plant diet (Allardyce & Linton, 2010).

A pair of lateral teeth plates, along with other ossicles, participate in food grinding and maceration (Brösing, 2010; Carvalho et al., 2018; Davie et al., 2015). Therefore, the morphology of the median and lateral teeth plate is a useful indicator for determining the substrate types associated with the habitats of deposit-feeding crabs. This conclusion aligns with Brösing and Türkay (2011), who proposed that comparisons of the gastric teeth across different taxa and their morphological similarities suggest a potential correlation with feeding behavior. Moreover, that the teeth within the gastric mill exhibit a comparatively stable ground pattern that may encompass adaptation tailored to specific food preferences or resources.

4.2 | Teeth morphology of gastric mills in phylogenetic context

In our observations, *T.* aff. *ceratophora* exhibit notable similarities not only in terms of external morphology but also in terms of habitat preferences to *I. orientalis* and *I. strigicarpus*. Despite this resemblance, phylogenetic trees indicate that *Tmethypocoelis* is more closely related
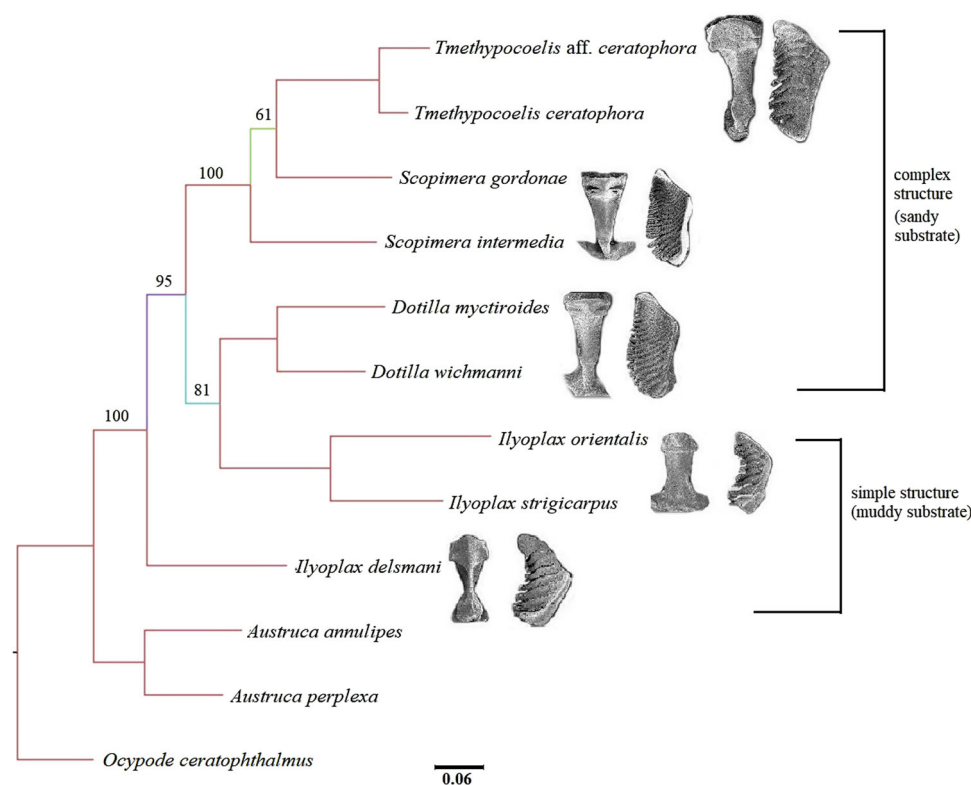
FIGURE 7 Maximum likelihood tree of dotillid crabs based on a concatenated sequence data set of 550 bp of 16S and 613 bp of COI with mapping of gastric mill teeth.

to *S. gordonae* rather than to *Ilyoplax* (Figure 7). Additionally, the morphology of the median tooth in *T.* aff. *ceratophora* is more similar to that of *S. gordonae* and *S. intermedia*. These findings support the phylogenetic tree results and aligns with the findings of Brösing and Türkay (2011) that phylogenetic groups built from gastric mill morphology are similar to those built from the examination of other phylogenetically important characters, such as gonopods. Scholtz (2014) also concluded that morphological characters, such as foregut ossicles, clearly resolve the phylogenetics of brachyuran crabs.

On a preliminary basis, we mapped gastric mill morphology onto the molecular phylogenetic tree constructed by Tsang et al. (2014; Figure 8), incorporating data from three sections and five families mainly sourced from Brösing (2010): Dromiacea (Dromiidae, Dynomenidae, Homolidae), Raninoida (Raninidae), and Cyclodorippoida (Cymonomidae). In the lateral tooth plate of the gastric mill, there are 8 teeth in *Dromia personata* (Dromiidae), 5 teeth in *Paradynomene tuberculata* (Dynomenidae), 4 teeth in *Homola ranunculus* (Homolidae), 12 teeth in *Raninoides hendersoni* (Raninidae), and 3 teeth in *Cymonomus granulatus* (Cymonomidae) (Brösing, 2010). These species have simple structure of propyloric ossicles on the median tooth (Figure 8). In our study, species inhabiting mud flats have similar simple structure of propyloric ossicles to those of species inhabiting sandy flats. In other intertidal crab species, *Mictyris longicarpus* (Mictyridae) has 23 teeth (Brösing, 2010) and *Austruca perplexa* (Ocypodidae) has 14 teeth (Naderloo et al., 2010) on the lateral tooth plate. Moreover, these species have complex structure of propyloric ossicles on the median tooth plate.

From these limited data, however, it is quite difficult to assess evolutionary trend of this morphology. Furthermore, gastric mills presumably perform strong adaptation to ecological aspect, and therefore their morphology might be affected by process of convergent evolution. Further study is necessary to elucidate the evolutionary trajectory of this morphology.

4.3 | Evolution on the teeth morphology

The difference in tooth morphology can be classified as macroevolution, with distinct phenotypic differences observed at the genus level. Within a genus, the numbers of teeth on the median tooth and lateral tooth plates exhibit similarity, but the characteristics of these teeth differ between species. Macroevolution encompasses the origin of novel characteristics or the history and causes of evolutionary patterns at higher taxonomic levels over genealogical time spans (Futuyma, 1998). For example, the formation of the flattened carapace in brachyuran crabs occurred under various circumstances during evolution, such as adaptation to water currents, living in crevices or benthic habitats, avoiding predation, and manipulating prey (Scholtz, 2014). Therefore, our plausible conclusion is that the teeth morphology of dotillid crabs resulted from adaptive modification based on their habitats, especially the substrate types. The alteration of tooth morphology is exemplified by Figures 7 and 8. Among these dotillid crabs, *D. myctiroides* has the most complex lateral tooth plate, and *S. gordonae* has the most complex median tooth plate. The
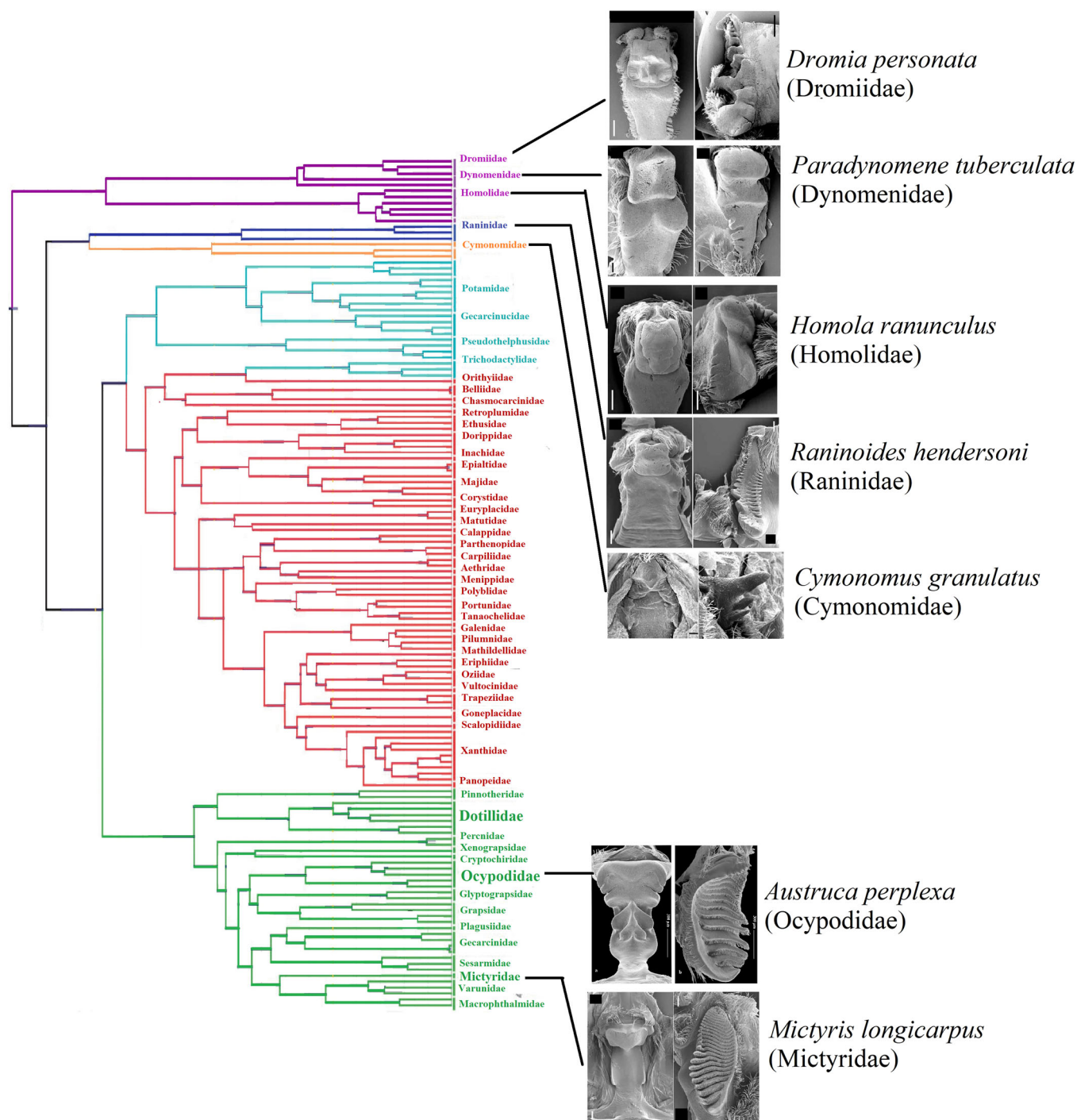
FIGURE 8 Maximum clade credibility from Tsang et al. (2014) and teeth on gastric mill from Brösing (2010) and Naderloo et al. (2010).

most complex structure is considered to be the most derived and to have undergone late diversification (Camargo et al., 2017).

5 | CONCLUSION

The teeth morphology of the gastric mill is a character useful in distinguishing genera and species among dotillid crabs. Despite essentially having a similar feeding behavior, species of dotillid crabs differ from each other in terms of the morphology of the median tooth plate and lateral tooth plates. These teeth support the phylogenetic tree. However, more data on the teeth of the gastric mill from other dotillid crabs need to be collected to postulate the plesiomorphic and apomorphic forms of these teeth. The median and lateral tooth plates are useful in ascertaining the substrate types of the habitats of deposit-feeding crabs, with a larger number of teeth on the lateral teeth implying occupation of sandy substrata and a smaller number implying occupation of muddy substrata. Species of

Dotilla and *Scopimera* feed on sand particles and require an efficient "mortar and pestle" to crush and grind these HP. In contrast, species of *Ilyoplax* feed primarily on mud and are more generalized in their ability to squash soft food particles.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are not available in any repository.

ORCID

Dewi C. Murniati http://orcid.org/0000-0002-4920-0578

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/jmor.21605.

REFERENCES

Allardyce, B. J., & Linton, S. M. (2010). Functional morphology of the gastric mills of carnivorous, omnivorous, and herbivorous land crabs. *Journal of Morphology*, *271*, 61–72. https://doi.org/10.1002/jmor.10781

Allen, C. J. (2010). *Ecology of the intertidal crab Dotilla intermedia from tsunami impacted beaches in Thailand*. PhD thesis, University of Southampton.

Balss, H. (1934). Die Krabben der Reise J. W. Harms' nach der Christmas-Insel und dem Malaiischen Archipel. *Zoologischer Anzeiger*, *106*(10), 225–237.

Brösing, A. (2010). Recent developments on the morphology of the brachyuran foregut ossicles and gastric teeth. *Zootaxa*, *2510*, 1–44.

Brösing, A., Richter, S., & Scholtz, G. (2007). Phylogenetic analysis of the Brachyura (Crustacea, Decapoda) based on characters of the foregut with establishment of a new taxon. *Journal of Zoological Systematics and Evolutionary Research*, *45*, 20–32.

Brösing, A., & Türkay, M. (2011). Gastric teeth of some thoracotreme crabs and their contribution to the brachyuran phylogeny. *Journal of Morphology*, *272*, 1109–1115. https://doi.org/10.1002/jmor.10967

Camargo, T. R., Rossi, N., Castilho, A. L., Costa, R. C., Mantelatto, F. L., & Zara, F. J. (2017). Sperm ultrastructure of shrimps from the family Penaeidae (Crustacea: Dendrobranchiata) in a phylogenetic context. *Arthropod Structure & Development*, *46*, 588–600.

Camroux, D., & Jaffrelot, C. (2021). The concept of the Indo Pacific in the Geostrategic Discourse. Retreived March 31, 2023, from https://www.sciencespo.fr/ceri/en/content/lindo-pacifique-quels-contours-quels-enjeux

Carvalho, D. A., Collins, P. A., Lima-Gomes, R., Magalhães, C., Torres, M. V., & Williner, V. (2018). A comparative study of the gastric ossicles of Trichodactylidae crabs (Brachyura: Decapoda) with comments on the role of diet and phylogeny in shaping morphological traits. *PeerJ*, *6*, e5028. https://doi.org/10.7717/peerj.5028

Darriba, D., Taboada, G. L., Doallo, R., & Posada, D. (2012). JModelTest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772.

Davie, P. J. F. (1990). New and rare crabs of the subfamily Dotillinae (Crustacea: Ocypodidae) from Northern Australia and Papua New Guinea. *Memoirs of the Queensland Museum*, *28*, 463–473.

Davie, P. J. F., Guinot, D., & Ng, P. K. L. (2015). Anatomy and functional morphology of Brachyura. Chapter 71-2, pp. 11–163. In P. Castro, P. J. F. Davie, D. Guinot, F. R. Schram, & J. C. Von Vaupel Klein (Eds.), *Decapoda: Brachyura (Part 1). Treatise on zoology—anatomy, taxonomy, biology. The Crustacea* (Vol. 9C-I, p. 638). Brill.

De Man, J. G. (1887–1888). Report on the podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Andersondr F.R.S., Superintendent of the Museum. *Journal of the Linnean Society, London (Zoology)*, *22*, 1–312.

De Man, J. G. (1892). Decapoden des indischen Archipels. In M. Weber (Ed.), *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien* (Vol. 2, pp. 265–527). Zweiter Band.

De Man, J. G. (1926). *Ilyoplax delsmani* n. sp., a new species of Ocypodidae. *Zoologische Mededelingen, Leyden*, *9*(1), 16–27.

Lima-Gomes, R. C., de Farias Lima, J., & Magalhães, C. (2017). Description of ten additional ossicles in the foregut of the freshwater crabs Sylviocarcinus pictus and Valdivia serrata (Decapoda: Trichodactylidae). *Zoologia*, *34*, 1–7. https://doi.org/10.3897/zoologia.34.e13731

Dewi, K., & Purwaningsih, E. (2020). Three new species of Cloacininae (Nematoda: Strongyloidea) parasitic in *Dorcopsis muelleri* (Schlegel, 1866) from Papua and Salawati Island, Indonesia. *Zootaxa*, *4747*(3), 535–546.

Felgenhauer, B. E., & Abele, L. G. (1989). Evolution of the foregut in the lower Decapoda. In B. E. Felgenhauer, L. Watling, & A. B. Thistle (Eds.), *Functional morphology of feeding and grooming in Crustacea. Crustacean Issues 6* (pp. 205–219). A.A. Balkema.

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*, 294–299.

Futuyma, D. J. (1998). *Evolutionary biology* (3rd ed., p. 763). Sinauer Association, Sunderland.

Gherardi, F., Russo, S., & Lazzara, L. (2002). The function of wandering in the sand-bubbler crab, *Dotilla fenestrata*. *Journal of Crustacean Biology*, *22*(3), 521–531.

Huang, J. F., Yang, S. L., & Ng, P. K. L. (1998). Notes on the taxonomy and distribution of two closely related species of ghost crabs, *Ocypode sinensis* and *O. cordimanus* (Decapoda, Brachyura, Ocypodidae). *Crustaceana*, *71*, 942–954.

Huxley, T. H. (1884). *The crayfish: An introduction to the study of zoology* (p. 731). Kegan, Paul & Trench.

Icely, J. D., & Jones, D. A. (1978). Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African shore. *Estuarine and Coastal Marine Science*, *6*, 315–325.

Kindpng. (2010). Peta Indonesia. Retrieved March 31, 2023, from https://www.kindpng.com/imgv/ThhJbxm_peta-indonesia-png-transparent-png/

Kitaura, J., & Wada, K. (2006). New species of *Ilyoplax* (Brachyura: Ocypodidae: Dotillinae) from the Philippines and Indonesia: behavioral, molecular and morphological evidence. *The Raffles Bulletin of Zoology*, *54*(2), 373–379.

Koelbel, K. (1897). Beschreibung der Krebse. *Wissenschaftliche Ergebnisse der Reise des Grafen Béla Széchenyi in Ostasien*, *2*, 709–718.

Lee, S. L., & Lim, S. S. L. (2004). Do diameters of burrows and food pellets provide estimates of the size structure of a population of *Dotilla myctiroides* at the sand-flats of Ao Tung Khen. Pukhet? *Phuket Marine Biological Research Center Bulletin*, 65, 56–60.

Milne Edward, H. (1834). *Histoire naturelle des Crustacés comprenant l'anatomie, la physiologie et la classification de ces animaux*. Librairie Encyclopédique de Roret. https://www.biodiversitylibrary.org/item/54621#page/523/mode/1up

Milne Edwards, H. (1852). Observations sur les affinités zoologiques et la classification naturelle des Crustacés. *Annales des Sciences Naturelles*, 18(3), 109–166.

Naderloo, R., Türkay, M., & Chen, H. L. (2010). Taxonomic revision of the wide-front fiddler crabs of the *Uca lactea* group (Crustacea: Decapoda: Brachyura: Ocypodidae) in the Indo-West Pacific. *Zootaxa*, 2500, 1–38. https://doi.org/10.11646/zootaxa.2500.1.1

Nauck, E. (1880). Das Kaugerüst der Brachyura (mit Beschreibung neur Gattungen und Arten, z. T. von C. Semper). *Zeitschrift Wissenchaftliche Zoologie*, 1, 1–69.

Rossi, F., & Chapman, M. G. (2003). Influence of sediment on burrowing by the soldier crab *Mictyris longicarpus* Latreille. *Journal of Experimental Marine Biology and Ecology*, 289, 181–195.

Sakai, K., & Türkay, M. (2013). Revision of the genus *Ocypode* with the description of a new genus, *Hoplocypode* (Crustacea: Decapoda: Brachyura). Memoirs of the Queensland Museum. *Nature*, 56(2), 665–793.

Sakai, K., Türkay, M., & Yang, S. L. (2006). Revision of the *Helice/Chasmagnathus* complex (Crustacea: Decapoda: Brachyura). *Abhandlungen der Senckenbergischen Naturforschenden Geselschaft*, 565, 1–76.

Scholtz, G. (2014). Evolution of crabs—History and deconstruction of a prime example of convergence. *Contributions to Zoology*, 83(2), 87–105.

Serène, R., & Moosa, M. K. (1981). Description de *Scopimera gordonae* sp. nov. (Crustacea, Decaposa, Brachyura), une espece des eaux orientales d'Indonesie. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, 53(1), 1–9.

Shih, H. T. (2015). *Uca (Xeruca)*, a new subgenus for the Taiwanese fiddler crab *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), based on morphological and molecular evidence. *Zootaxa*, 3974(2), 151–169.

Shih, H. T., Kamrani, E., Davie, P. J. F., & Liu, M. Y. (2009). Genetic evidence for the recognition of two fiddler crabs, Uca iranica and U. albimana (Crustacea: Brachyura: Ocypodidae), from the northwestern Indian Ocean, with notes on the U. lactea species-complex. *Hydrobiologia*, 635, 373–382.

Shih, H. T., Lee, J. H., Ho, P. H., Liu, H. C., Wang, C. H., Suzuki, H., & Teng, S. J. (2016). Species diversity of fiddler crabs, genus *Uca* Leach, 1814 (Crustacea: Ocypodidae), from Taiwan and adjacent islands, with notes on the Japanese species. *Zootaxa*, 4038, 057–082.

Shih, H. T., Naruse, T., & Ng, P. K. L. (2010). Uca jocelynae sp. nov., a new species of fiddler crab (Crustacea: Brachyura: Ocypodidae) from the Western Pacific. *Zootaxa*, 2337(1), 47–62.

Shih, H. T., Ng, P. K. L., & Christy, J. H. (2015). *Uca (petruca)*, a new subgenus for the rock fiddler crab *Uca panamensis* (Stimpson, 1859) from Central Africa, with comments on some species of the American broad-fronted subgenera. *Zootaxa*, 4034(3), 471–494.

Takagi, K. K., Cherdsukjai, P., Mimura, I., Yano, Y., Adulyanukosol, K., & Tsuchiya, M. (2010). Soldier crab (*Dotilla myctiroides*) distribution, food resources and subsequent role in organic matter fate in Ao Tang Khen, Phuket, Thailand. *Estuarine, Coastal and Shelf Science*, 87, 611–617.

Trivedi, J. N., Soni, G. M., Trivedi, D. J., & Vachhrajani, K. D. (2015). A new species of *Ilyoplax* (Decapoda, Brachyura, Dotillidae) from Gujarat, India. *Journal of Asia-Pacific Biodiversity*, xxx, 1–5.

Trivedi, J. N., & Vachhrajani, K. D. (2018). On new record of brachyuran crab *Scopimera crabicauda* Alcock, 1900 (Crustacea: Decapoda) from India. *Journal of the Marine Biological Association of India*, 60(1), 105–107.

Tsang, L. M., Schubart, C. D., Ahyong, S. T., Lai, J. C. Y., Au, E. Y. C., Chan, T. Y., Ng, P. K. L., & Chu, K. H. (2014). Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution*, 31(5), 1173–1187. https://doi.org/10.1093/mdbev/msu068